LATE ORDOVICIAN TRILOBITES FROM SOUTHERN THAILAND

by RICHARD A. FORTEY

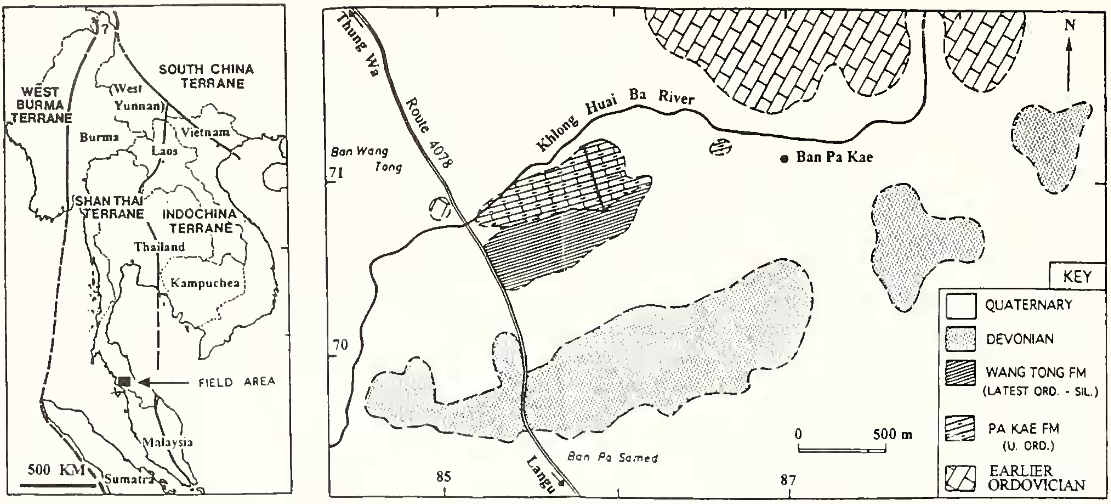
ABSTRACT. A rich and well-preserved trilobite fauna is described from the upper Ordovician (Caradoc) Pa Kae Formation, Satun Province, southern Thailand. This is the first diverse trilobite fauna of this age to be described from the Shan Thai (Sibumasu) terrane. The fauna represents an outer shelf assemblage of 39 species, dominated by *Ovalocephalus*, nileids and remopleuridids. It is identical even at the species level to faunas described from the Pagoda Limestone of southern China, indicating that the Shan Thai terrane cannot have been far removed geographically from this part of China in the late Ordovician. The distribution of the *Ovalocephalus* fauna proves that there are also wider faunal links with western Gondwana and Scandinavia. Most of the species have been previously named from China, but new information is presented for several of them. Examination of the agnostid *Arthrorhachis latelimbata* proves that cell polygons are a much finer-scale structure than reticulate sculpture. The telephinid *Telephina convexa* has holochroal eyes constructed of perfectly square lenses: the possibility that these represent reflection superposition eyes is considered. Two new species are proposed: *Sculptaspis pulcherrima* and *Ovalocephalus plewesae*.

VERY little has been published on Ordovician trilobites from Thailand (Stait *et al.* 1984), and no late Ordovician fauna has been described hitherto. The Pa Kae Formation (Wongwanich *et al.* 1990) is a distinctive unit of red-weathering limestones cropping out in the southernmost Satun Province of Thailand, close to the Malaysian border (Text-fig. 1). Dr C. Burrett and T. Wongwanich discovered trilobites in this unit in 1986, and in 1987 the author visited the type section (Text-fig. 2), which was then entirely clear of vegetation, and collected many more specimens. A second visit was made in 1994, at which time the lower part of the section had already become obscured under a vigorous growth of rubber trees. Not only did the fauna prove to be a new one for the Shan Thai terrane, but it is also well preserved, which makes a systematic account worthwhile. Previous descriptions of the species have mostly been in Chinese journals which are hard to obtain in the West. Nearly all the trilobite genera are described from the Shan Thai block for the first time, and several are recorded for the first time outside the Yangtze Platform. The palaeogeographical position of the Shan Thai terrane in the Palaeozoic is the subject of controversy (Metcalfe 1992), and the palaeobiogeography of the trilobite faunas contributes to our understanding of the position of this region in the late Ordovician.

THE PA KAE FORMATION

The Pa Kae Formation crops out in a small area of Satun Province, southern Thailand (Wongwanich *et al.* 1990). The type section (Text-fig. 1) is a small hill about half a kilometre east of the main road (Route 4078) along the track to the village of Ban Pa Kae, which is itself about 10 km north of the town of Langu, La Ngu District. On the 1:50,000 map sheet, Amphoe Langu (reference 49221), the outcrop occupies the area between grid references 8583 7122 and 8592 7085. This is at 6° 58′ 25″ N, 99° 46′ 42″ E. The Pa Kae Formation is the uppermost limestone formation in the Ordovician sequence of southern Thailand. Almost all the collections described here were made from the type section, which can be identified by conspicuous red bluffs by the side of the track.

[Palaeontology, Vol. 40, Part 2, 1997, pp. 397–449, 10 pls]



TEXT-FIG. 1. Locality map of the Pa Kae Formation in southern Thailand (right) with South-east Asian terranes indicated on left hand diagram, with modern national boundaries.

Field characteristics. The lower part of the Pa Kae Formation comprises massive pelmatozoan limestones from which no trilobites have been collected. These produce a prominent topographical feature, and the base of the section shown in Text-figure 2 is taken above these conspicuous beds. The overlying strata are comparatively well-bedded, red-weathering muddy limestones which form a series of small bluffs: bed-by-bed collecting was possible through much of this section. The limestones are notable for their syneresis cracks which form conspicuous polygons standing proud from the surrounding limestone. Some particularly ferruginous horizons contain patches of haematite, a mineral which also commonly lines stylolite seams. Although the impure limestones often appear dense and structureless, where there is appropriate weathering there are indications of extensive bioturbation. Orthoconic nautiloids occur in several beds.

Instead of being concentrated into lenses or particular beds, the trilobites appear to be scattered sparingly throughout the limestones. Much breaking of rock is required to obtain a good number of specimens. In most beds they are exquisitely preserved (see, for example, Text-fig. 4). Although fully articulated specimens have not been collected, there is a fair number of cephala which retain their free cheeks; this is an indication that the trilobites have probably not been greatly reworked, and that the species found probably lived together *in situ*. The comparatively large number of specimens about 10 mm long or less in the collections may be partly an artefact of the collecting technique. The rocks are so hard and even grained that the trilobites do not crack out. The collections were made by progressively breaking collected limestone blocks to cubes of side 10 mm and then manually preparing any specimens showing on the surface. This method provides a good sample per volume, but also biases against larger specimens.

There is a sparse fauna of brachiopods accompanying the trilobites which is referable to the *Foliomena* fauna (Cocks and Rong 1988, p. 67).

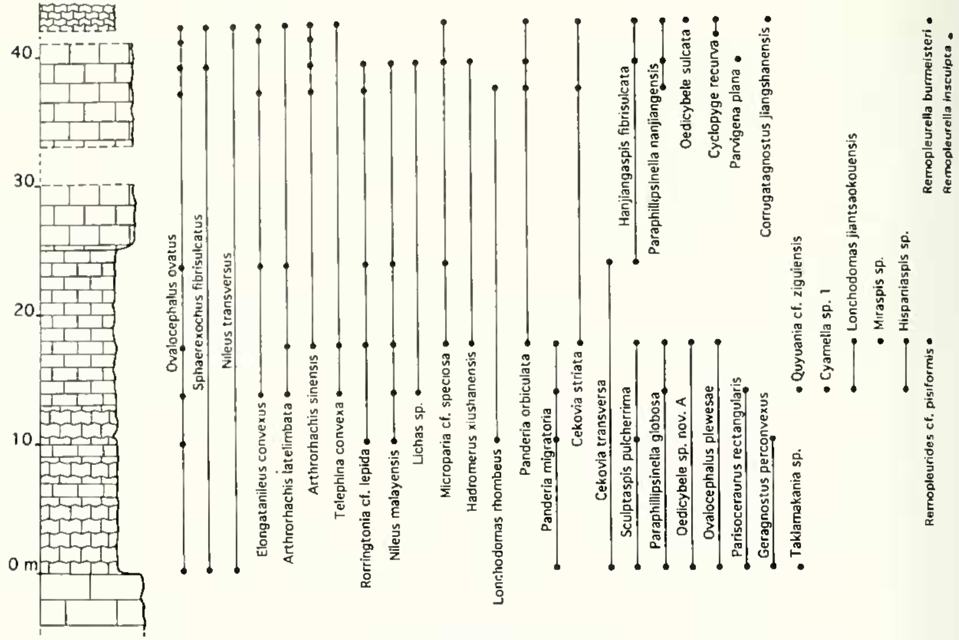
Depositional environment. The lithology and fauna (see below) of the Pa Kae Formation appear to be identical to that of the Pagoda Limestone Formation, which is widespread across central and south-western China. In the past, this formation has been regarded as of shallow water origin, because the polygonal cracks abundantly developed within it have been thought to be desiccation cracks. Ji (1985) has pointed out that these are better interpreted as syneresis cracks. These are formed in clay-rich sediments beneath continuous water cover (Burst 1965). The *Foliomena* brachiopod fauna is regarded as the deepest water one in the latest Ordovician (Cocks and Rong 1988), and Boucot (pers. comm. 1994) places it in his Benthic Assemblage 4. Ji (1985) states that the water depth under which the Pagoda Limestone was deposited may have been 70–100 m.

The trilobites represent a rich fauna: *Ovalocephalus* is the commonest genus, *Paraphillipsinella*, *Remopleurella*, agnostids and nileids are numerous, while the other genera are represented by small numbers of specimens. However, cyclopygids and *Telephina* are present, both elements of an open ocean pelagic fauna (Fortey 1985). Price and Magor (1984) portrayed a shallow to deep water biofacies profile for the Ashgill of North Wales: an assemblage dominated by *Dindymene*, cyclopygids and telephinids typified a deep water, but not deepest, biofacies (where a dominance of cyclopygids and blind trilobites was typical). Nileids and raphiophorids occupied a similar depth zone to that of the Pa Kae Formation in the earlier Ordovician (Fortey 1975*a*). Atheloptic trilobites having reduced eyes (Fortey and Owens 1987) are uncommon in the Pa Kae Formation, and the benthic part of the fauna is dominated by trilobites with normal eyes. It seems very likely, therefore, that the sea floor was within the photic zone, and probably at a depth of 200 m or less. This seems to agree with Ji's (1985) estimate, based on sedimentary features of the Pagoda Limestone Formation. Benthic brachiopods are present, along with the trilobites, and there are also gastropods, bivalves and rare echinoderms. This rich fauna, combined with the evidence for bioturbation (possibly also the oxidation state of the iron compounds, if original) surely indicates a well oxygenated sea floor. This may be the reason why graptolites are not preserved, although they are numerous in the black shales succeeding the Pa Kae Formation (Wongwanich *et al.* 1990).

AGE AND CORRELATION OF THE PA KAE FORMATION

The fauna of the Pa Kae Formation may be divided into a lower one and an upper one (Text-fig. 2); the latter yields more prolific fossils. However, several species, including *Sphaerexochus fibrisulcatus* and *Ovalocephalus ovatus*, range throughout, and there are overlapping species ranges in the mid-part of the collected section, both of which suggest continuous deposition over a comparatively short period. With rare species, one must be cautious about sampling effects artificially truncating the true length of ranges (Strauss and Sadler 1989). However, the Pa Kae Formation is apparently confacial throughout, and there are stratigraphically related species changes through the section in the agnostids, and in certain genera (e.g. *Ovalocephalus*, *Panderia*, *Remopleurella*), which suggest that the changes observed are of biostratigraphical value.

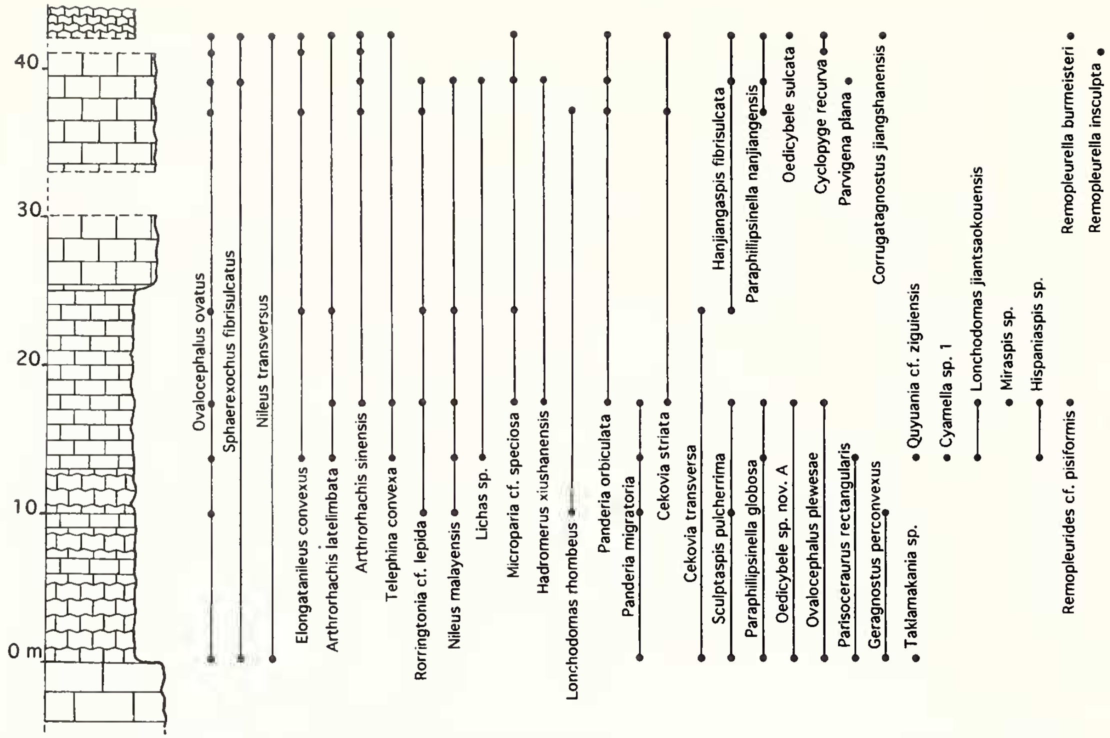
The lower fauna shares several species with the small fauna described by Kobayashi and Hamada (1978) from Langkawi Island, not far to the south. The species *Geragnostus perconvexus* and *Lonchodomas rhombeus* are significant in proving this correlation, while *Nileus* species are also similar. Neither of the first two species has been recorded from the Pagoda Limestone Formation in southern China. Kobayashi and Hamada (1978, p. 1) were imprecise as to the age of the Langkawi Island fauna stating that it was 'in a range from middle Caradoc to early Ashgill'. There are two species definitely found both in the lower fauna and in Bed 12 of the Chedao Formation of Gansu Province, China (Zhou and Dean 1986): *Ovalocephalus plewesae* sp. nov. (identified by Zhou and Dean as *O. kelleri* Koroleva) and *Paraphillipsinella globosa*. In the systematic section, I also suggest that *Lonchodomas nanus* Zhou and *Nileus huanxianensis* Zhou from the Chedao Formation may prove to be junior synonyms of species from the Pa Kae Formation. Zhou and Dean (1986, p. 744) listed many additional species of trilobites and associated cephalopods from Bed 12 as evidence for its correlation with the Pagoda Limestone Formation of the Yangtze region, which is regarded as of Caradoc age (Zheng *et al.* 1983; Chen *et al.* 1995). Hence a correlation of the lower fauna with some part of the Pagoda Limestone Formation is likely. The Langkawi Island faunule is therefore also likely to be Caradoc.



TEXT-FIG. 2. Section through the upper part of the Pa Kae Formation at its type locality showing ranges of trilobites within the section. Base of the measured section is taken above massive crinoidal limestones forming the lower part of the formation.

The upper fauna is identical in many respects to that of the Pagoda Limestone Formation of southern China (Lu 1975; Ji 1986; Sheng and Ji 1987; Zhou and Xiang 1993). A great majority of the whole list of species is in common, including a number of distinctive forms which are known nowhere else but in the Pagoda and Pa Kae formations. These latter include: *Elongatanileus convexus*, *Remopleurella insculpta*, *Cyclopyge recurva*, *Parvigena plana*, *Hanjiangaspis fibrisulcata*, *Quyuania* cf. *ziguiensis*, *Panderia orbiculata*, *Hadromeros xiushanesis* and *Sphaerexochus fibrisulcatus*. Geographically more wide-ranging species, some of which have ranges extending into strata equivalent to the lower Ashgill, include *Corrugatagnostus jiangshanensis*, *Nileus transversus*, *Remopleurella burmeisteri*, *Microparia speciosa*, *Telephina convexa*, *Paraphillipsinella globosa*, *P. nanjiangensis*, *Oedicybele sulcata*, *Ovalocephalus ovatus* and *Parisoceraurus rectangularis*. Ji (1986, p. 8) noted that *Ovalocephalus ovatus* and both *Paraphillipsinella* species are present in all Pagoda Limestone Formation localities in Sichuan, Guizhou, Shaanxi, Hubei and Anhui provinces. There can be no doubt at all that the Pa Kae Formation and the Pagoda Limestone are correlative. At the southern edge of the northern China platform (Ordos Basin, Shaanxi Province) faunas comparable to those of the Pagoda Limestone Formation intergrade with graptolitic facies (Fu *et al.* 1993), and this indicates a correlation with the *Climacograptus bicornis* Biozone. Wang (*in* Chen *et al.* 1995, p. 64) cited evidence that the Pagoda Formation 'ranges through the interval from the *D. clingani* Zone to the lowest part of the *P. linearis* Zone', i.e. is Caradoc. However, Sheng and Ji (1987) concluded that the top of the Pagoda Formation may extend into the lower Ashgill.

The Pagoda Limestone in China does not appear to have been formally divided biostratigraphically, although, as described above, there is some evidence to suggest that two successive



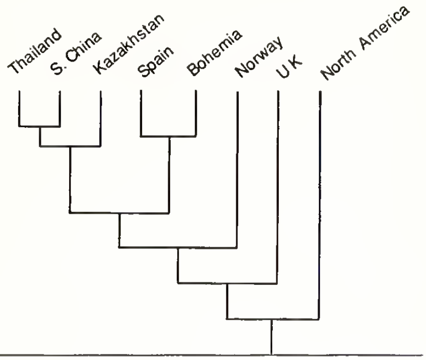
TEXT-FIG. 2. Section through the upper part of the Pa Kae Formation at its type locality showing ranges of trilobites within the section. Base of the measured section is taken above massive crinoidal limestones forming the lower part of the formation.

The upper fauna is identical in many respects to that of the Pagoda Limestone Formation of southern China (Lu 1975; Ji 1986; Sheng and Ji 1987; Zhou and Xiang 1993). A great majority of the whole list of species is in common, including a number of distinctive forms which are known nowhere else but in the Pagoda and Pa Kae formations. These latter include: *Elongatanileus convexus*, *Remopleurella insculpta*, *Cyclopyge recurva*, *Parvigena plana*, *Hanjiangaspis fibrisulcata*, *Quyuania* cf. *ziguiensis*, *Panderia orbiculata*, *Hadromeros xiushanesis* and *Sphaerexochus fibrisulcatus*. Geographically more wide-ranging species, some of which have ranges extending into strata equivalent to the lower Ashgill, include *Corrugatagnostus jiangshanensis*, *Nileus transversus*, *Remopleurella burmeisteri*, *Microparia speciosa*, *Telephina convexa*, *Paraphillipsinella globosa*, *P. nanjiangensis*, *Oedicybele sulcata*, *Ovalocephalus ovatus* and *Parisoceraurus rectangularis*. Ji (1986, p. 8) noted that *Ovalocephalus ovatus* and both *Paraphillipsinella* species are present in all Pagoda Limestone Formation localities in Sichuan, Guizhou, Shaanxi, Hubei and Anhui provinces. There can be no doubt at all that the Pa Kae Formation and the Pagoda Limestone are correlative. At the southern edge of the northern China platform (Ordos Basin, Shaanxi Province) faunas comparable to those of the Pagoda Limestone Formation intergrade with graptolitic facies (Fu *et al.* 1993), and this indicates a correlation with the *Climacograptus bicornis* Biozone. Wang (*in* Chen *et al.* 1995, p. 64) cited evidence that the Pagoda Formation 'ranges through the interval from the *D. clingani* Zone to the lowest part of the *P. linearis* Zone', i.e. is Caradoc. However, Sheng and Ji (1987) concluded that the top of the Pagoda Formation may extend into the lower Ashgill.

The Pagoda Limestone in China does not appear to have been formally divided biostratigraphically, although, as described above, there is some evidence to suggest that two successive

TABLE 1. (Left) Comparison of species and genera in common with Chinese faunas (expressed as percentage of Pa Kae fauna), to show identity with the Pagoda Limestone Formation. For the purpose of this comparison, provisional determinations (cf., ?, etc) are regarded as conspecific. (Right) Dendrogram showing relationship of Pa Kae trilobitefauna to those from other areas as expressed in decreasing numbers of genera in common.

Formation	Sichuan (Pagoda)	Guizhou (Pagoda)	Shaanxi (Pagoda)	Hubei (Pagoda)	Anhui (Pagoda)	Zhejiang (Huanigang)	Gansu (Chedao)
Species (%)	15	10	44	35	8	10	13
Genera (%)	29	18	61	61	15	25	39



faunas can be recognized in its Thai equivalent (see Text-fig. 2). The earlier fauna has among the commoner species, *Ovalocephalus plewesae*, *Panderia migratoria*, *Geragnostus perconvexus* and *Sculptaspis pulcherrima* confined to it, while several rarer species have also only been recovered from the earlier part of the section, providing additional, but less reliable, evidence of stratigraphical differentiation. Interestingly, *Paraphillipsinella globosa* is the common form in the early fauna, *P. nanjiangensis* in the later, although this is apparently not so in China. I have no intention of recognizing formal subdivisions here, except to note that it is likely that more refined regional correlation should prove attainable.

As for direct evidence for correlation outside the Far East, *Remopleurella burmeisteri* from the upper fauna was originally described from the uppermost Caradoc (Onnian Substage of the Streffordian Stage; see Fortey *et al.* 1995) of the type area in Shropshire (Dean 1963). It was described subsequently from the Solvang Formation of the Oslo Region, Norway (Nikolaisen 1983), from strata also believed to be of latest Caradoc age. *Panderia migratoria* was described by Bruton (1968) from the Upper Chasmops Shale of Norway (= Nakkholmen Formation) and the Skagen and Macrourus Limestone of Sweden. According to Owen *et al.* (1990), the Nakkholmen Formation is correlated with the Woolstonian to Actonian substages of the Caradoc (i.e. immediately pre-Onnian), which is consistent with the occurrence of *Panderia migratoria* below *Remopleurella burmeisteri* in Thailand. Thus, on the evidence of these few widespread species, it is considered that the Pa Kae Formation spans the upper half of the Caradoc Series (Cheneyan to Streffordian stages in the revision of Fortey *et al.* 1995).

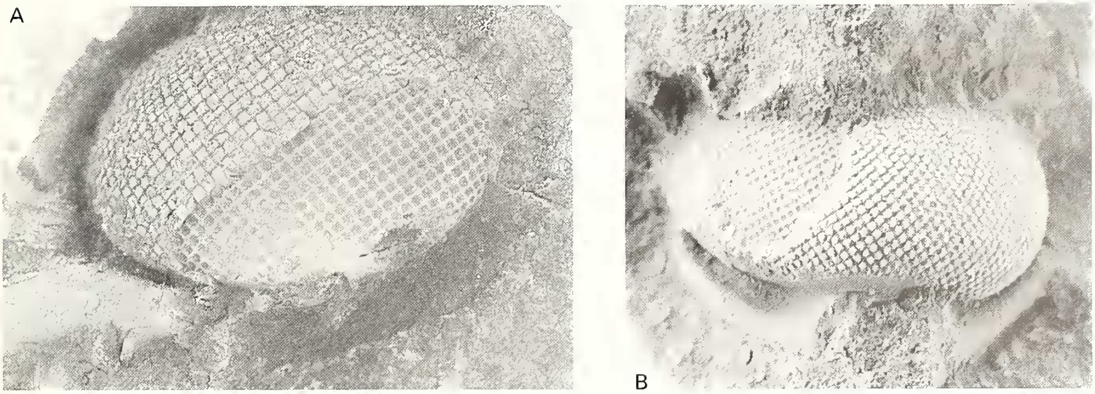
PALAEOGEOGRAPHY, TERRANES AND THE *OVALOCEPHALUS* FAUNA

South-east Asia comprises a complex arrangement of terranes with a varied Palaeozoic history. The locality from which the trilobites were collected is at the southern edge of the Sibumasu terrane (Metcalfe 1992), which is also referred to as the Shan Thai terrane (Burrett *et al.* 1990). The Pa Kae Formation contains the first rich fauna of late Ordovician age to be described from this terrane. Kobayashi and Hamada (1970, 1978) described a few species from Malaysia, including agnostids, cyclopygids and nileids, which are pandemic taxa in the later Ordovician and hence of little use in critically determining palaeogeographical position. However, a cyclopygid-dominated assemblage does indicate a deep water biofacies, and is often associated with sites marginal to ancient continents or microcontinents.

The new Thai fauna is identical at the species level to that from the Pagoda Formation, which is distributed through Sichuan, Guizhou, Shaanxi and Hubei provinces in southern China. Table 1 shows that the greatest similarity of the Thai fauna is to faunas from Shaanxi Province (Upper Yangtze Platform), by comparison with the recent Pagoda trilobite fauna compilations of Ji (1986) and Zhou and Xiang (1993). The last named authors informed me (pers. comm. 1994) that there are several biofacies distinguishable within the Pagoda Formation *sensu lato* and this may account for the similarity to Shaanxi in particular. However, even though certain genera are widely distributed beyond China, the Thai fauna includes so many *species* in common with southern China that its biogeographical signature can scarcely be questioned. Many of these species are endemic to the region; if one excludes taxa (such as *Nileus* spp.) with which there are outstanding taxonomic problems, reliable endemics include: *Arthrorhachis latelimbata*, *Corrugatagnostus jiangshanensis*, *Elongatanileus convexus*, *Remopleurella insculpta*, *Taklamakania* spp., *Lonchodomas jiantsaokouensis*, *Parvigena plana*, *Hanjiangaspis fibrisulcata*, *Telephina convexa*, *Paraphillipsinella nanjiangensis*, *Quyania* sp., *Panderia orbiculata*, *Oedicybele sulcata*, *Ovalocephalus ovatus*, *Hadromeros xiushanensis*, *Parisoceraurus rectangularis* and *Sphaerexochus fibrisulcatus*. Even allowing for the possibility of wider distribution of Ordovician shelf faunas, this long list of species identities, coupled with the lithological similarities, would usually be taken as good evidence that the Sibumasu terrane should have been close to, or even contiguous with, the Yangtze Platform in the late Ordovician (Cocks and Fortey 1988, Fig. 7). Five genera, *Hanjiangaspis*, *Parisoceraurus*, *Elongatanileus*, *Taklamakania* and *Quyania*, are so far known only from Shan Thai and southern China.

This alleged proximity does not match some hypotheses of Ordovician terrane distribution. Burrett *et al.* (1990) and Metcalfe (1992, fig. 4), for example, in their early Ordovician reconstructions, show the Sibumasu terrane close to the palaeoequator, with South China at about 45° South. The North China block is also much closer to Sibumasu on these reconstructions, both being within the tropics, while South China is positioned in the southern temperate zone. Taking the faunal evidence alone the present evidence would rather support a switch of the positions of the North and South China blocks relative to the Sibumasu (Shan Thai) terrane, which would minimize their palaeolatitudinal difference by placing Sibumasu and South China close together on the palaeoequator. Alternatively, if the terranes were left in the same relative positions as by Metcalfe (1992), the same effect might be accomplished by a reorientation of the whole of this part of Gondwana later in the Ordovician relative to palaeolatitude, such that Sibumasu, North and South China (plus Tien Shan and Indochina) would become close to the same palaeolatitude rather than spanning several latitudinal belts. However, Burrett *et al.* (1990, fig. 4) showed several faunal elements in common between South China and Sibumasu even in the *early* Ordovician, which they apparently attribute to a northward-flowing ocean current displacing temperate water masses towards the tropical belt. There is no critical evidence to decide between these different explanations of faunal similarity as regards the present fauna, although the extraordinary similarity of the Thai fauna to those of the Yangtze Platform is beyond question, and might favour geographical proximity over the distributive effects of ocean currents.

Dean and Zhou (1988), Zhou and Dean (1989) and Hammann (1992) have noticed the wide distribution of a trilobite fauna which includes the peculiar and distinct genus *Ovalocephalus*. The earlier Ordovician history of *Ovalocephalus* appears to be in eastern Asia (Lu and Zhou 1979) extending to Kazakhstan (Koroleva 1959*a*). It spread rapidly westwards in the Ashgill as far as Poland (Kielan 1960), Sardinia (Leone *et al.* 1991) and Spain (Hammann 1992). 'Absence' evidence is often problematical, but the Caradoc faunas of western Europe are so well-known that it seems improbable that the absence of *Ovalocephalus* from that area in pre-Ashgill strata is a failure of collection, and thus that its movement westwards was a real phenomenon. Tripp *et al.* (1989) have commented on the many trilobite species that are closely similar between southern China (Tangtou Formation) and Poland (*Staurocephalus clavifrons* Zone) in the Ashgill, which attests to freedom of distribution through much of Gondwana at that time (cf. Dean 1967). The fact that some individual species in the present fauna, notably *Remopleurella burmeisteri* and *Panderia migratoria*, extend from Thailand as far as Scandinavia, shows that wide distribution was possible even in the Caradoc. There are additional species that point to an earlier phylogenetic history of certain taxa in eastern Asia. I describe below a proetide which I attribute to *Parvigena* Owens, a hitherto enigmatic form previously known only from the Boda Limestone (Ashgill, Sweden). *Remopleurella insculpta* Ji represents an 'ancestral' morphology both for *R. burmeisteri* and the widespread Ashgill genus *Amphitryon*. Both these examples indicate that towards the end of the Ordovician other taxa probably accompanied *Ovalocephalus* in a westward spread. However, both *Panderia* (see Bruton 1968) and *Sculptaspis* (see Nikolaisen 1983) have an earlier history in Scandinavia and these presumably spread *eastwards* at the same time. Taken together, this provides evidence that there was a more general distribution of trilobite faunas as a whole in the late Caradoc. However, none of the trilobites described herein is related to the controversial species from Vietnam and Yunnan, of Bohemian identity, which are the subject of the 'affaire Deprat' (Henry 1994). Because these terranes are placed closed to Sibumasu on all reconstructions (Metcalfe 1992), it does seem unlikely that their alleged faunas are so different, and this may be additional, if circumstantial evidence of the bogus status of the Deprat collection.



TEXT-FIG. 3. Eyes of the trilobite *Telephina convexa* Lu, showing perfectly square lenses, lateral views. A, It 25429, × 8, 42 m; B, It 25878, × 8, 18 m; internal moulds show that the lenses were square on the inner surface also.

A TRILOBITE EYE WITH SQUARE LENSES

Several specimens of large, holochroal trilobite eyes have been collected (Text-fig. 3) which show perfectly square lenses. This unusual feature merits some discussion here rather than in the systematic section.

The eye in question belongs to a *Telephina* species, all of which have large lenses. *Telephina pustulata* Ulrich, 1930, seems to show a similar pattern of square lenses. *Telephina americana* (Billings, 1865) (see Whittington 1965, pl. 37, figs 15–16) shows a less perfect arrangement of square lenses apparently admixed with some hexagonal ones anteriorly. The primitive telephinid *Oopsites* has hexagonal lenses, as does the related genus *Carolinites* (see Fortey 1975*b*), so it seems that square lenses may be a derived character of at least some *Telephina* species. Ji (1986) has recorded two species from the Pagoda Limestone, which has a fauna identical in other respects to that of the Pa Kae Formation; the Thai species is assigned to *T. convexa* Lu, 1975.

The possible function of these curious lenses is interesting. Like trilobites with holochroal eyes, most living arthropods with compound eyes have hexagonal lenses, and the great majority of these function as apposition eyes, in which each lens captures an image of a discrete, small angle of space. An exception is many, perhaps all, of the macruran crustaceans (including carid and pennaeid shrimps and lobsters; Vogt 1980). These have perfectly square lenses. In such crustaceans the sides of the lenses are silvered to form a reflecting 'box'. Land (1984) described their function as reflecting superposition eyes: by reflection from the sides of the 'box', light falling on each facet is brought to a common focus. Only perfectly square lenses have this property; silvering simply will not work to a common focus with 120° angles.

This opens up the intriguing possibility that this Ordovician eye could offer the earliest example of a superposition eye in the fossil record. Land (1981) has shown that the square lenses in *Palaemonetes* were only acquired late in ontogeny, earlier growth stages being hexagonal, so a 'switch' from apposition to superposition is not phylogenetically difficult, and the fact that most trilobite eyes were probably apposition eyes is no serious objection. Land (1984, p. 434) observed that 'it is probably true that eyes with a wholly square facet lattice are of the reflecting superposition type'.

However, there are problems with this interpretation for the eye of *Telephina convexa*. In the first place, the eye is obviously not spherical, as it is in the Recent reflecting examples, and this is a necessary condition for producing a satisfactorily focused image. Second, it is unclear how reflection would work with calcite as the medium (M. F. Land, pers. comm. 1988). Conventional trilobite lenses have the c-axis of the calcite lens normal to its surface and permitted unrefracted light to pass through along that axis to stimulate the rhabdom. It is difficult to see how the reflecting 'box' system could work under these constraints. The interpretation of these remarkable eyes therefore provides a considerable challenge.

SYSTEMATIC PALAEONTOLOGY

Newly described figured material is deposited in the collections of The Natural History Museum, London. Terminology follows that of Moore (1959) except that the glabella is understood to include the occipital ring. Because many of the species have been described elsewhere I have kept the descriptions to the bare minimum, and devoted more attention to comparative remarks. A few examples of the Thai material show better preservation than known hitherto, and fuller descriptions are given of such species. Systematic order is by family, following the modifications to Moore (1959) introduced by Fortey (1990). Stratigraphical ranges are given in Text-figure 2.

EXPLANATION OF PLATE 1

Figs 1, 4. *Corrugatagnostus jiangshanensis* (Lu, 1964). 1, It 25392; cephalic shield, 4, It 25853; pygidium. Both 42 m; × 10.

Fig. 2. *Arthrorhachis tarda* (Barrande, 1846); Schary Collection 1920, Museum of Comparative Zoology, Harvard; dorsal exoskeleton; note deep border furrows compared with the following figures; Kosov Mts, Czech Republic, Kraluv̊ Dvůr Formation, upper Ordovician (Ashgill); × 7.

Figs 3, 5–6, 8–10, 13–14. *Arthrorhachis latelimbata* (Ji, 1986), 3, 6, 9, It 25276; dorsal, lateral and anterior views of cephalic shield with narrowest border; note lack of deep border furrows; 24 m; × 16; 5, 8, It 25510; cephalic shield in dorsal and lateral views (see also Text-fig. 3); 18 m; × 12; 10, 13–14, It 25275; pygidium, posterior, lateral and dorsal views; 42 m; × 8.

Figs 7, 11–12. *Geragnostus perconvexus* (Kobayashi and Hamada, 1978). 7, It 25175; cephalic shield; 10·4 m. 11–12, It 25467; pygidium, incomplete, dorsal and lateral views, 0·6 m. All × 12.

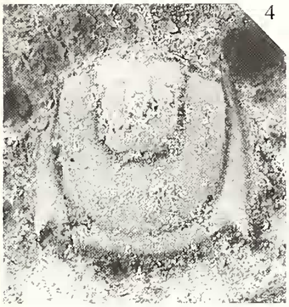
All, except figure 2, from Satun Province, southern Thailand; Pa Kae Formation, upper Ordovician (Caradoc); figures given in metres are heights above base of section.

PLATE 1


1


2


3


4


5


6


7


8


9


10


11


12


13


14

FORTEY, Ordovician trilobites

Family METAGNOSTIDAE Jaekel, 1909

Genus ARTHRORHACHIS Hawle and Corda, 1847

Type species. Agnostus tardus (Barrande, 1846), by monotypy.

Remarks. The type species has often been referred to *Trinodus* M'Coy, 1845. Fortey (1980) observed that the type and only specimen of the type species of *Trinodus*, *T. agnostiformis* M'Coy, which is a poorly preserved cephalic shield, shows none of the critical features used to identify metagnostids to genus. Additional material from the type locality has not yet been described. Accordingly, Fortey (1980) proposed that *Trinodus* should be restricted to the type specimen, and that *Arthrorhachis*, with the better known type species, *A. tarda*, be used to accommodate the appropriate Ordovician agnostids. This procedure has been followed in subsequent treatments of the group as a whole (Shergold *et al.* 1990; *pace* Pek and Prokop 1984), and is used again here. Morris (1988, p. 25) noticed that there is a problem over the lectotype selection of *A. tarda* (by Přibyl *in* Horný and Bastl 1970, erroneously described as holotype by Pek 1977). This lectotype is a complete specimen figured by Barrande (1852, pl. 49, figs 1–2) from Libomysl. However, the original (1846) description mentioned no complete specimens, and the locality given there ('pres de Beroun') is likely to refer to Kralův Dvůr (in Czech = Königshof, in German), which has furnished many of the specimens incorporated into museum collections, including those of the National Museum in Prague and The Natural History Museum, London. It seems likely that the Libomysl specimen was not among Barrande's original syntypes, and hence not available for selection as lectotype. Whittington (1950) figured some of the Kralův Dvůr (as Königshof) specimens.

Arthrorhachis latelimbata (Ji, 1986)

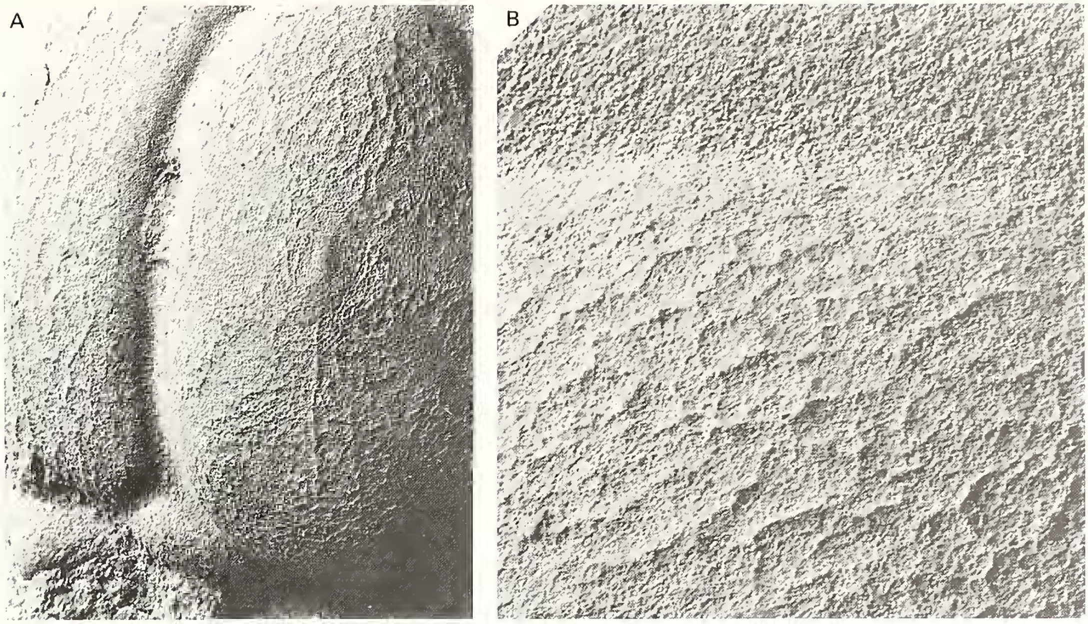
Plate 1, figures 3, 5–6, 8–10, 13–14; Text-figure 4

1986 *Trinodus latelimbatus* n. sp. Ji, p. 11, pl. 1, fig. 5.

Material. Cephalic shields: It 25210, 25276, 25276, 25510; pygidia: It 25208, It 25275, It 25901.

Stratigraphical range. Upper part of Pa Kae Formation section, 14·4–42 m above base.

Description. Ji (1986, p. 11) briefly described this species from a pygidium. A cephalic shield is associated here and is probably the best preserved one of this genus yet known. It has been examined with a SEM (Text-fig. 4) and shows several details. Muscle impressions are shown to be elliptical, smooth areas and four pairs of such areas are visible in front of the occipital ring. The most posterior pair slopes rather steeply backwards, the second pair less so, while the third pair is nearly transverse, adjacent to the median glabellar tubercle. The anterior pair is directed anterolaterally; there may be a small additional impression between the second and third pairs adjacent to the axial furrow. These impressions are clearly homologous with those noted on internal moulds of *Arthrorhachis danica* by Fortey (1980). The glabellar tubercle lies a little in front of glabellar mid-length. Behind the tubercle there is a pair of narrow ridges which diverge outwards from the tubercle to the level of the posterior muscle impressions. I am not aware of these having been described from any other agnostid. There is a surface sculpture comprising a raised reticulum on the dorsal cuticular surface, which fails to extend into the circum-glabellar furrows, on to the border, or into the muscle impressions. Such a reticulum is present on well-preserved material that has been compared with *A. tarda* (Kielan 1960, pl. 1, fig. 10; Owen and Bruton 1980, pl. 1, fig. 1), but is also present on *Galbagnostus galba* (Billings) (see Whittington 1965, pl. 3, figs 7, 15) and *Arthrorhachis elspethi* (Cooper) (see Hunt 1967, pl. 22, fig. 44), and may prove to be rather common on metagnostids. However, at a very much finer scale (10–15 μm; see Text-fig. 4) there is a polygonal pattern which extends generally, including into the muscle impressions. This pattern is likely to reflect cell polygons, such as have been described on *Homagnostus obesus* by Wilmot (1990). Agnostids seem to have unusually thin exoskeletons (Fortey and Wilmot 1991) and this may assist the ready visibility of such cell polygons. This specimen does, however, prove that the surface reticulum has nothing to do with cell polygons.



TEXT-FIG. 4. *Arthrorhachis latelimbata* (Ji, 1986); It 25510; details of cephalic shield on Plate 1, figure 5; scanning electron micrographs. A, glabellar muscle impressions; × 50; B, fine cell polygons at minute scale compared with reticulate sculpture; × 150.

The border furrow is shallow, little more than a change in slope. On the specimens with the widest border, the border itself is slightly less than half the width (sag.) of the preglabellar field; in these, preglabellar field and border together comprise three-eighths of the total cephalic length. However, there are specimens with a narrower border which show identical sculpture and development of the border furrow; these are also assigned to *A. latelimbata*, which is assumed to be variable in this character.

The pygidium has a similarly shallow border furrow and some specimens show an equally wide border, which is gently convex. Posterolateral marginal spines are minute. The short axis is equal to, or slightly longer than the postaxial field (sag.), gently tapering to a somewhat truncate terminal piece. Transverse ring furrows are shallow and obscure in this species; the terminal piece is about twice as wide as long. The median tubercle is developed on the posterior part of the median axial lobe.

Remarks. Late Ordovician *Arthrorhachis* are usually referred to *A. tarda* (Barrande). A specimen of this species from the type locality is figured here for comparison (Pl. 1, fig. 2; see also Pek 1977). It shows deep marginal border furrows, in the condition described in other agnostids as deliquiate (Shergold *et al.* 1990, p. 11). This is not an artefact of preservation, because other agnostids which have been compared with *A. tarda*, preserved in full relief, also show the same feature (e.g. Dean 1971; Owen and Bruton 1980, pl. 1, fig. 1; Ahlberg 1989). The presence of a deliquiate border has been used as a distinguishing generic feature in Cambrian agnostids. *A. tarda*-like specimens from China have been referred to *A. sinensis* Sheng, 1964, by Zhou (1987), who noted (p. 656) that '*A. tarda* may well be a senior synonym of *A. sinensis*'. The Thai material assigned herein to *A. latelimbatus* shows a shallow border furrow, both on cephalon and pygidium, and hence cannot be referred to *A. tarda* or to *A. sinensis*. Ji (1986) founded *A. latelimbata* upon two pygidia from the Pagoda Limestone Formation in Shaanxi Province, but the illustrated holotype clearly shows a similar wide border and narrow border furrow to those on the Thai material, and the axial characters are also comparable. The cephalic shield associated herein displays the same features of the cephalic border. It is possible that a species described by Chen (*in* Li *et al.* 1975) as *Trinodus* *cylindricus* may prove to be a senior synonym of *A. latelimbata* since it apparently shows a comparable border structure; however, the illustrations are inadequate to be certain of this.

Arthrorhachis sinensis (Sheng, 1964)

Plate 2, figures 1, 4

Synonymy. See Zhou 1987, p. 656.

Material. Cephalic shields, It 25209, 25277, 25295, 25900; pygidia, It 25302, 25393.

Stratigraphical range. Upper part of Pa Kae Formation section, 18–42 m above base.

Remarks. Zhou (1987) discussed fully the nomenclatural history of this species and noted that it may prove to be a synonym of *A. tarda*. The stratigraphical and geographical distribution of the latter was summarized by Tripp *et al*. (1989, p. 31). Most of the occurrences of *A. tarda* are from Ashgill strata. Zhou used the name *sinensis* for some *tarda*-like forms from China, and selected a lectotype for the species from the Pagoda Formation, of Caradoc age. Those specimens from the Pagoda Formation figured by Ji (1986) as *Geragnostus sinensis* would now be referred to *Corrugatagnostus jiangshanensis*. The specimens from the Pagoda Formation that correspond with *A. sinensis* were described by Ji (1986) as *Trinodus* aff. *tardus* (Barrande) and by Chen (*in* Li *et al*. 1975) as *Trinodus ovatus* Chen. To add to the confusion, the species from the Tangtou Formation (early Ashgill) was referred by Zhou (1987, p. 656) to *sinensis*, but by Tripp *et al*. (1989) to aff. *tarda* without further mention of *sinensis*. Clearly, the use of the name *A. sinensis* is not unequivocal. I employ it here because the material from the Pa Kae Formation is identical with 'aff. *tardus*' from the Pagoda Formation, the type of *sinensis* is also from that formation, and it is older stratigraphically than most records of *A. tarda*. A critical assessment of all records of these agnostids is needed to determine if *A. sinensis* is a valid species. Zhou (1987) placed *A. latilimbatus* Ju (*in* Qiu *et al*., 1983) into the synonymy of *A. sinensis*; this is known from an entire specimen. The posterior border furrow on the pygidium is narrower than it is on typical *A. tarda* (e.g. Kielan 1960; Pek 1977; Ahlberg 1989), and the same feature is shown on a specimen from the Pagoda Limestone illustrated by Ji (1986, pl. 1, fig. 4). This may prove to be a useful character in identifying *A. sinensis*.

Genus CORRUGATAGNOSTUS Kobayashi, 1939

Type species. *Agnostus morea* Salter, 1864, original designation; Llanvirn, Hope Shales, Shropshire.

EXPLANATION OF PLATE 2

Figs 1, 4. *Arthrorhachis sinensis* (Sheng, 1964). 1, It 25295; cephalic shield; × 12. 4, It 25393; pygidium; × 10. Both 42 m.

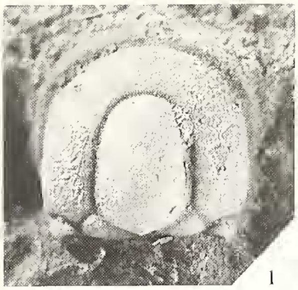
Figs 3, 8–9, 13. *Elongatanileus convexus* Ji, 1986. 3, It 25379; free cheek; 37 m; × 4; 8, It 25870; cranidium; 42 m; × 8; 9, It 25284, pygidium; 24 m; × 10. 13, It 25299; small pygidium; 24 m; × 7.

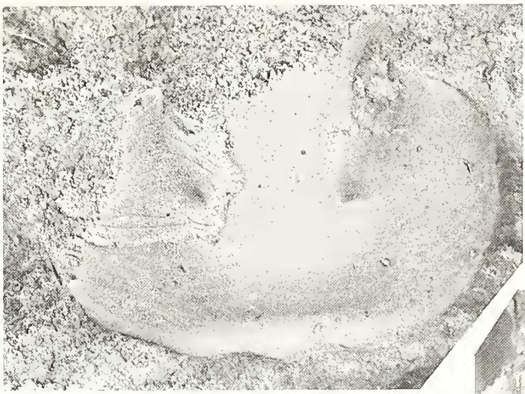
Figs 2, 5–7, 10–11. *Nileus malayensis* Kobayashi and Hamada, 1978. 2, It 25867; incomplete hypostome; 18 m; × 10. 5, It 25349; cranidium; 39 m; × 5. 6–7, It 25183; pygidium. 6, latex cast from external mould; 7, counterpart prepared to show doublure. Both 10·4 m; × 8. 10, It 25890; large free cheek; 18 m; × 5. 11, It 25352; free cheek, possibly associated with this species, retaining short genal spine; 39 m; × 4.

Figs 12, 14. *Nileus transversus* Lu, 1964; It 25484; pygidium, dorsal and posterior views; 0·6 m; × 5.

Specimen details as for Plate 1, figures 1, 3–12.

PLATE 2

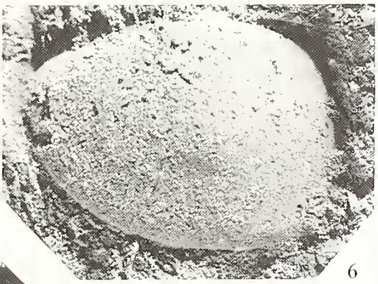

1


2


3


4


5


6


7

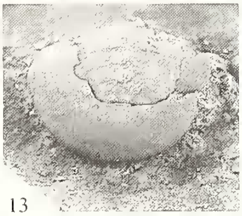

8


10


9


11


12


13


14

Corrugatagnostus jiangshanensis Lu, 1964

Plate 1, figures 1, 4

1986 *Geragnostus sinensis* Sheng; Ji, p. 11. pl. 1, figs 6–7.
1989 *Corrugatagnostus jiangshanensis* Lu; Tripp *et al*., p. 32, fig. 3*i*, *s*, *w*.

See Zhou (1987, p. 659) for earlier synonymy.

Material. Cephalic shield, It 25392; pygidium, It 25853.

Stratigraphical range. Uppermost part of Pa Kae Formation section, 42 m from base.

Remarks. This species was discussed fully by Zhou (1987) who included within it several other taxa described from Chinese material including much that had been named as *Geragnostus sinensis* Sheng, 1964. The well-preserved cephalic shield from Thailand is very like a specimen figured from the Pagoda Limestone described by Ji (1986, pl. 1, fig. 6) as *sinensis*, and should, following Zhou, be placed in *Corrugatagnostus jiangshanensis*. There are no scrobiculae on the Thai specimens as is also true for the material from the Pagoda Limestone figured by Ji (1986), and from the Tangtou Formation, Nanjing Hills, figured by Lu and Zhou (1981) and Tripp *et al*. (1989). The lectotype (see Lu *et al*. 1976, pl. 9, fig. 3) from the Huangnehkang Formation (early Ashgill) of Zhejiang is clearly scrobiculate. However, Zhou (1987, p. 658) states that this species is highly variable in this character in particular and 'many specimens have almost smooth genae'. If this is correct there is no reason to identity the Thai material as other than *C. jiangshanensis*, especially on the basis of the sparse material available.

Genus GERAGNOSTUS Howell, 1935

Type species. *Geragnostus sidenbladhi*, Linnarsson, 1869, by original designation; Tremadoc, Sweden.

Geragnostus perconvexus Kobayashi and Hamada, 1978

Plate 1, figures 7, 11–12

1978 *Geratrinodus perconvexus* Kobayashi and Hamada, p. 9, pl. 1, fig. 4*a–e*.
1978 *Geratrinodus levigatus* Kobayashi and Hamada, p. 9, pl. 1, fig. 5*a–d*.

Material. Cephalic shields, It 25175–25177, 25468–25469; pygidia, It 254467, 25470.

Stratigraphical range. Low in Pa Kae Formation section, 0·6–10·4 m above base.

Remarks. *G. perconvexus* was made the type species of a new genus *Geratrinodus* by Kobayashi and Hamada (1978). Fortey (1980) and Shergold *et al*. (1990) noted that this species was essentially an effaced *Geragnostus*, and preferred to assign *G. perconvexus* to that genus. In any case, the similarly effaced *Neptunagnostella* Pek, 1977 is a senior synonym of *Geratrinodus*. The type specimen of *G. perconvexus* is from Langkawi, Malaysia, close to the type section of the Pa Kae Formation. A cephalon figured here is identical to the holotype (see Kobayashi and Hamada 1978, pl, 1, fig. 6*a*). *G. levigatus* from a different bed on Langkawi is known from a somewhat more effaced pygidium. A certain variability in the degree of effacement is commonly found in agnostids, and it seems very likely that *levigatus* is an intraspecific variant of *perconvexus*.

Family NILEIDAE Angelin, 1854

Genus NILEUS Dalman, 1827

Type species. *Nileus armadillo*, Dalman, 1827, from the uppermost Arenig–lower Llanvirn of Sweden, by monotypy (see Nielsen 1995).

Nileus malayensis Kobayashi and Hamada, 1978

Plate 2, figures 2, 5, 6–7, 10–11

1978 *Nileus malayensis* Kobayashi and Hamada, p. 13, pl. 2, figs 2–4.
?1982 *Nileus huanxianensis* Zhou, p. 266, pl. 66, fig. 9.
?1986 *Nileus huanxianensis* Zhou; Zhou and Dean, p. 756, pl. 59, figs 3, 6; pl. 60, figs 1–6, 8, 11.

Material. Cranidium, It 25349; partial cephalon, It 25351; hypostome, It 25867; free cheeks, It 25868, 25890 (specimen with small genal spine, It 25352); pygidium, It 25183.

Stratigraphical range. Much of Pa Kae Formation section, 10·4–39 m from base.

Remarks. Kobayashi and Hamada (1978) based this species on sparse material, an incomplete cranidium and a free cheek, from Langkawi Island, Malaysia, geographically the closest Ordovician to that of the Pa Kae Formation. Additional material has been collected from Thailand, which is apparently identical with the Malaysian species, and the same name is used, even though the placement of the species within *Nileus* as a whole is not satisfactory. For example, Kobayashi and Hamada did not consider *N. platys* Schrank, 1972, from the Caradoc of Sweden, which has a similarly large eye and effaced glabella. *N. symphysuroides* Lu, 1957 (see Lu 1975, pl. 22, figs 8–10), from the Pagoda Limestone, is different in having a distinctly convex glabella. *N. rugosus* Xia, 1978 (see also Tripp *et al.* 1989, fig. 5*m*) may be another species to consider in relation to the Thai form, but I have been unable to determine whether Xia or Kobayashi and Hamada have priority. The foreword to volume 19 of *Geology and Palaeontology SE Asia* is dated January 1978, which, if it coincides with publication, would favour the priority of the latter. Even in fragmentary condition, the cranidium of *N. malayensis* is easily distinguished from that of any *Elongatanileus* species by its curved palpebral lobe, and more anteriorly positioned glabellar 'tubercle' (actually a thinning of the dorsal exoskeleton; see Fortey and Clarkson 1976). I have assigned to this species typical *Nileus* pygidia (Pl. 2, figs 6–7) which show a very broad axis, rapidly tapering, with three axial rings clearly visible. The doublure is broad, reflexed against the dorsal surface, and bears 10–12 terrace ridges. The ill-defined border occupies no more than one-quarter of the pygidial length, distinguishing it from the other Pagoda Limestone species, *N. transversus* Lu, 1957 (see Lu 1975, pl. 20, figs 21–22; Tripp *et al.* 1989, fig. 5), which has a relatively wide pygidium on which the border is well defined. *Nileus huanxianensis* Zhou, 1982 (see also Zhou and Dean, 1986, p. 756), from Bed 12 of the Chedao Formation, Gansu Province, China, is identical to *N. malayensis* (in so far as the material of that species permits judgement), and given that there are several other species in common between the lower part of the Pa Kae Formation and Bed 12 there is a case for synonymizing *N. huanxianensis* with *N. malayensis*. Little is known about what variation exists within any of these taxa, and none can be considered critically defined.

Nileus transversus Lu, 1957

Plate 2, figures 12, 14

1982 *Nileus transversis*; Koroleva, p. 105, pl. 21, figs 1–3.
1989 *Nileus transversus*; Tripp, Zhou and Pan, 1989, p. 37 [with synonymy].

Material. Pygidia, It 25484, 25492; hypostome, It 25488.

Stratigraphical range. Throughout the Pa Kae Formation section.

Remarks. Lu (1975) and Tripp *et al.* (1989) recently described this species, a familiar member of the Pagoda Limestone Formation fauna. The transversely wide pygidium with well-defined border are the specific characters cited by these authors. The Ashgill examples from the Tangtou Formation described by Tripp *et al.* (1989, fig. 5*v*–*w*) have a much more transverse anterior cranidial outline than does the cranidium assigned to the species by Lu (1975, pl. 22, fig. 12). Lesser differences have been accorded specific significance in the Nileidae. Koroleva (1982) erected a species, *Nileus transversis*, from the Caradoc of Kazakhstan, apparently unaware of the use of *transversus* as a specific name by Lu; the pygidia seem to be identical to those of the Chinese species.

Genus ELONGATANILEUS Ji, 1986

Type species. *Elongatanileus convexus* Ji, 1986, from the Pagoda Limestone, Hubei Province, South China, by original designation.

Remarks. This genus was founded, not very satisfactorily, on a cranidium, which is long (sag.) compared with that of *Nileus*. Other parts of the exoskeleton were unknown. I have discovered the type species also in Thailand, where it occurs with a pygidium which can be associated plausibly on account of its comparatively narrow axis. Ji (1986) did not make comparison with *Peraspis* Whittington, 1965 or *Poronileus* Fortey, 1975*a*, when he erected *Elongatanileus*, even though both these genera are clearly more similar to it than is *Nileus*. This applies to the elongate cranidium, spinose free cheek (cf. *Peraspis*) and to the pygidium, which is like that of *Poronileus isoteloides* Fortey, 1975*a*, from the lower middle Ordovician Valhallfonna Formation, Spitsbergen. I provisionally retain *Elongatanileus* here because it shows two features which are different from *Poronileus*: (1) the very low divergence of the preocular sutures produces an evenly rounded, as opposed to anterolaterally angulate, anterior cranidial profile; and (2) the postocular cheek is so short (tr.) that maximum cranidial width is at the palpebral lobes (*Poronileus* cranidia are widest at the posterior margin). These features suggest that *Elongatanileus* shares a common ancestor with *Nileus*, in which both these features can be found. Instead, *Poronileus* was related to *Peraspis* by Fortey (1975*a*). *Peraspis* species have a better defined glabella than *Elongatanileus*, and transverse pygidia with pleural furrows. Finally, the genus *Aocaspis* was erected by Dolambi and Gond (1991) for an early Ordovician species from the Montagne Noire, without comparison with *Elongatanileus*, of which the authors may have been unaware. It has a better defined glabella, and transverse pygidium compared with those of *Elongatanileus*.

Elongatanileus convexus Ji, 1986

Plate 2, figures 3, 8–9, 13

1986	*Elongatanileus convexus* Ji, p. 15 (29), pl. 3, figs 1–2.
1987	*Elongatanileus convexus* Ji; Sheng and Ji, pl. 2, figs 10–11.

Material. Cranidia, It 25241, 25282, 25414, 25870; free cheek, It 25379; pygidia associated, It 25284, 25299, 25431, 25869; immature pygidia, It 25395–25396.

Stratigraphical range. Upper part of Pa Kae Formation section, 14·4–42 m above base.

Description. Ji's (1986) description was perfunctory, and in Chinese. A short description is therefore given here. The cranidium is two-thirds as wide as long, the maximum width being at the palpebral lobes. Orientation of specimens for measurement and illustration is in palpebral view (Bruton 1968) whereby the palpebral lobes are orientated horizontally. Since the cranidium has low even convexity (sag.) this orientation approximates to the usual, dorsal orientation. The dorsal surface is virtually featureless, showing no sign of axial or glabellar furrows. The very large palpebral lobes are gently curved, and approach half the cranidial length. The preocular divergence of facial sutures is very low, about 10° to sag. line; suture continues adaxially in a rather even curve, such that the anterior outline of the cranidium is a smooth convex arc about the mid-line. Postocular cheeks are reduced to tiny, triangular areas. There is an inconspicuous median tubercle opposite the posterior ends of the palpebral lobes at one-quarter cranidial length. I have associated a free cheek which has a narrow border, well defined for a nileid, and a prominent genal spine.

The pygidium is associated because it has nileid form, and has the indications of a long axis which seems to be an appropriate match for the cranidium. The narrow, tapering axis is clear on a small specimen, on which it extends to almost three-quarters pygidial length; the border is distinct. The pygidium is about 0·6 as long as wide. The axis occupies just under half the width at the anterior margin; facets do not reach it. The surface is smooth, lacking surface sculpture of any kind.

Remarks. The Thai cranidium figured is similar to the holotype. It is suggested that the comparative length of the cranidium is a function of the relative growth of the anterior, preocular part. This is because the median glabellar tubercle retains a relatively posterior position as it does on some *Poronileus* species. If the length had been attained by, as it were, pushing forward the whole cranidium, then the tubercle should have finished up farther anteriorly.

Family REMOPLEURIDIDAE Hawle and Corda, 1847

Genus REMOPLEURELLA Dean, 1963

Type species. Remopleurides burmeisteri Bancroft, 1949, upper Caradoc, Shropshire, England, by original designation.

Remopleurella burmeisteri (Bancroft, 1949)

Plate 3, figures 1–6, 8

Material. Cranidia, It 25493, 25859, 25861–25863; hypostome, It 25865; free cheeks, It 25257, 25424; pygidia, It 25423, 25255, 25509, 25864, 25902.

Occurrence. Uppermost part of the Pa Kae Formation section, 42 m above base.

Description. A full description and synonymy of this species were given by Dean (1963) and Nikolaisen (1983). The Thai material does reveal the pygidial doublure particularly well (Pl. 3, fig. 5), showing it to be broad, subhorizontal, extending close to the axis, with relatively sparse terrace ridges which curve backwards about the mid-line. These pygidial terraces are much less dense than those on the dorsal surface of the cranidium.

Remarks. Apart from having a broader glabellar tongue, *Remopleurella* is very like *Amphitryon* Hawle and Corda, 1847. Since this is likely to be a plesiomorphic character, this casts doubt on the value of recognizing *Remopleurella* as a distinct genus. Dean (1963, p. 251) selected a lectotype for *Remopleurella burmeisteri*, an internal mould of a cranidium from the late Caradoc Onnian Substage of Shropshire, England, and described additional material. Better preserved material identified with *R. burmeisteri* was described by Nikolaisen (1983) from Norwegian specimens from the uppermost part of the Solvang Formation, showing the sculptural features of the cranidium and the form of the pygidium. This material affords the closest comparison with the Thai specimens, from which no significant points of difference can be discovered, and, if Nikolaisen was correct in determining the Norwegian material as the same as that from Shropshire, then the same specific name must also be applied to the species from the Pa Kae Formation. In particular, it is noticeable that the rather dense terrace lines on the cranidium are backward-curved rather gently across the mid-line on the posterior part of the cranidium, and similar terrace lines extend on to the palpebral rims. The degree of incision of the glabellar furrows is also identical. It seems possible that

Amphitryon zhejiangensis Ji, 1986, from the Pagoda Limestone of Zhejiang, China, may prove identical, but this is difficult to judge on the basis of material so far illustrated.

Remopleurella insculpta (Ji, 1986)

Plate 3, figure 7

1986 *Remopleurides insculptus* Ji, p. 12, pl. 1, figs 10–11; pl. 2, fig. 2.

Material. Cranidia, It 25325–25326; hypostome, It 25357.

Stratigraphical range. High in Pa Kae Formation section, 41 m from base.

Remarks. The cranidium of this species is very like that of *R. burmeisteri*, from which it most obviously differs in lacking the beautiful bertillon pattern. The tongue protrudes more strongly forwards, so that in dorsal view it takes up more than one-third of the preoccipital preglabellar length (sag.); the anterior outline is semicircular rather than arcuate. The cranidium figured here is identical to that figured by Ji (pl. 1, fig. 6) apart from having slightly shallower glabellar furrows, and I have no doubt that the same species is represented. Clearly it should also be referred to the same genus as *R. burmeisteri*. In the Pa Kae Formation it stratigraphically underlies *R. burmeisteri*. In China it has been found in the Pagoda Limestone in Shaanxi Province.

Genus REMOPLEURIDES Portlock, 1843

Type species. *Remopleurides colbii* Portlock, 1843; middle Caradoc, Ireland, subsequently designated by Miller (1889).

Remopleurides cf. *pisiformis* Weber, 1948

Plate 3, figure 11

Material. Cranidium, It 25860.

Stratigraphical range. Pa Kae Formation section, 18 m above base.

Remarks. Although incomplete, this single *Remopleurides* cranidium is distinctive because it has an exceedingly broad glabellar tongue for the genus, combined with a short palpebral lobe and a surface sculpture of raised ridges. Koroleva (1982) redescribed *R. pisiformis* Weber, from the Caradoc of Kazakhstan, which shows the same features, including sculpture (Koroleva 1982, pl. 9, fig. 1). The glabella of some of the Kazakh forms appears to be even wider and the palpebral lobe narrower, but one of the cranidia figured by Koroleva (pl. 8, fig. 4) is very like the Thai specimen, and the same species name is provisionally used. No hypostome is known; if it has a long fork, the species may prove referable to *Hypodicranotus*.

EXPLANATION OF PLATE 3

Figs 1–6, 8. *Remopleurella burmeisteri* (Bancroft, 1949). 1–2, It 25493; cranidium in dorsal and anterior views; × 8; 3–4, It 25424; free cheek, dorsal and lateral views; × 7. 5, It 25423; pygidial doublure; × 12. 6, It 25859; incomplete cranidium; × 7. 8, It 25509; pygidium, dorsal view; × 9. All 42 m.

Fig. 7. *Remopleurella insculpta* (Ji, 1986); It 25325; cranidium; 41 m; × 12.

Figs 9–10, 12–13. *Sculptaspis pulcherrima* sp. nov. 9, 13, holotype, It 25196; large cranidium in anterior and dorsal views; × 10. 10, It 25910; thoracic segment; × 14. 12, It 25199; small cranidium; × 12. All 10·4 m.

Fig. 11. *Remopleurides* cf. *pisiformis* Weber, 1948; It 25860; cranidium; 18 m; × 10.

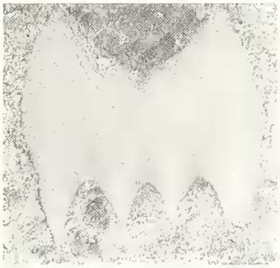
Specimen details as for Plate 1, figures 1, 3–12.


1


2


4


3


5

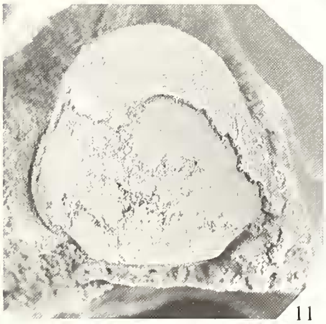

6

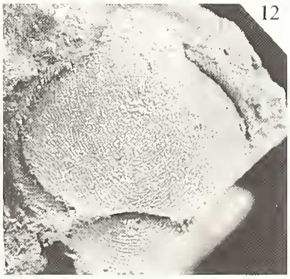

7


8


9


10


11


12


13

FORTEY, *Remopleurella*, *Sculptaspis*, *Remopleurides*

Genus SCULPTASPIS Nikolaisen, 1983

Type species. Sculptaspis cordata Nikolaisen, 1983, from the Arnestad and Frognerkilen Formation (formerly Lower Chasmops Shale and Lower Chasmops Limestone), Oslo district, Norway, by original designation.

Sculptaspis pulcherrima sp. nov.

Plate 3, figures 9–10, 12–13; Text-figure 5

Derivation of name. Latin, most beautiful, referring to the sculpture.

Holotype. Cranidium, It 25196.

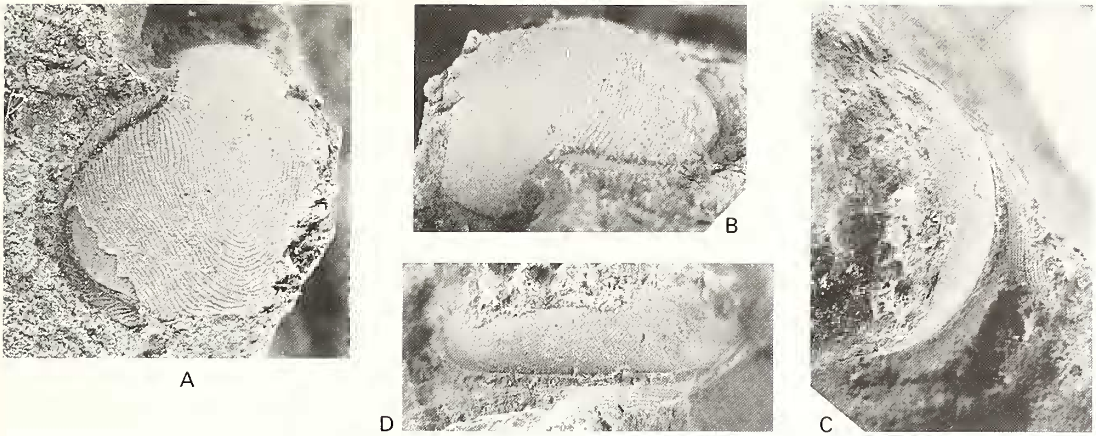
Material. Cranidia, It 25197, 25199, 25501, 25911; free cheek, It 25201; probable thoracic segment, It 25910.

Stratigraphical range. Lower part of Pa Kae Formation section, 0·6–18·0 m above base.

Diagnosis. Sculptaspis species having sculpture on glabella consisting solely of fine lines. Occipital ring about one-third length (sag.) of glabella in front. Glabellar furrows hardly defined dorsally.

Description. The cranidia show a consistent sculptural pattern which distinguishes them from other remopleuridid species from Thailand, Glabella profile is flat (sag., tr.) with a steeply downturned tongue. Preoccipital glabella has slightly wider maximum width (tr.) than length (sag.). Width of tongue is one-third maximum glabellar width, and in dorsal view the tongue is very gently convex forward. Palpebral lobes narrow, even for a remopleuridid. Occipital ring one-third of length of glabella in front, and a little more than twice as wide as long. Median tubercle at forward edge of ring. Surface sculpture of very fine lines arranged in a deep 'V' along the midline; there are no granules or tubercles admixed. On the occipital ring they are gently bowed rearwards. I have associated a free cheek with this species which carries similar sculpture on the border. The genal spine is advanced in position, and short, triangular. The lateral genal border has become extremely reduced and narrow (tr.). The long eye is of the usual strip-like remopleuridid form, but long and low (up to 25 minute lenses in a vertical row). Beneath the eye there is a wire-like eye socle. The extreme narrowness of the free cheek makes it likely that the pleurae on the thorax (see Pl. 3, fig. 10) were similarly abbreviated (tr.), since there is a direct relationship between genal width and thoracic width in remopleuridids. The whole exoskeleton in *Sculptaspis* was therefore probably unusually narrow and elongate, even in comparison with *Remopleurides*. The pygidium is likely to have been minute; this may explain why none has yet been assigned to *Sculptaspis*.

Remarks. Nikolaisen (1983) provided a good description of cephalic material of *S. erratica* from the Llanvirn Elnes Formation (= Ogygiocaris Shale) of Norway, a species which is closely similar to *S. pulcherrima. Sculptaspis* species have characteristic patterns of surface sculpture on their cranidia, and the sculptural pattern of the Norwegian and Thai species are alike, except that the former has granules along the edge abutting the palpebral furrow, which are lacking in the latter. There are several additional differences between the Norwegian and the Thai material which are of specific importance: the occipital ring is longer (sag.) in the species from the Pa Kae Formation – one-third as opposed to one-fifth the length of the preoccipital glabella; also the fine sculptural lines are more strongly rearward-curved medially, anteriorly on the Thai specimens, while faint remnant glabellar furrows remain on the dorsal surface of the Norwegian species, which are lost on the Thai form (they remain visible on internal moulds). Other species described by Nikolaisen (1983) have stronger glabellar furrows and different sculpture patterns. Note that the cranidium described by Kobayashi and Hamada (1978) from Langkawi as *Remopleurides* cf. *emarginatus* Törnquist (*emerginatus* [*sic*] on their plate explanation) cannot be conspecific with our species as it includes pits in the surface sculpture. Of species named from the Pagoda Limestone, the cranidium of *Remopleurides xixiangensis* Zhou (*in* Li *et al.*, 1975) resembles that of *Sculptaspis pulcherrima* in its general proportions, but the original illustrations are not adequate for a proper comparison. The original author has kindly sent me photographs of further material of this species which shows a shorter (sag.) occipital ring and less rearward-bowed raised lines on the glabella.



TEXT-FIG. 5. *Sculptaspis pulcherrima* sp. nov. A–B, It 25197; dorsal and oblique lateral views of incomplete cranidium showing sculpture. C–D, It 25201; dorsal and lateral views of free cheek showing advanced genal spine and very narrow border. Both 10·4 m; × 12.

Family CYCLOPYGIDAE Raymond, 1925

Genus CYCLOPYGE Hawle and Corda, 1847

Type species. Egle rediviva Barrande, 1846, upper Ordovician, Bohemia, by monotypy.

Cyclopyge recurva Lu, 1962

Plate 4, figures 1–5

1962 *Cyclopyge recurva* Lu, p. 53, pl. 20, figs 5–6, 9.
1975 *Cyclopyge recurva* Lu; Lu, p. 377, pl. 30, figs 6–12.

Material. Cranidia, It 25318, 25871–25872; pygidia, It 25319, 25873–25874.

Stratigraphical range. High in the Pa Kae Formation section, 41–42 m above base of section.

Remarks. Lu (1975) fully described this species, which is from the Pagoda Formation in south Shensi. He noted that *C. recurva* is distinguished by the recurved anterior part of the cranidium, at which the facial sutures converge nearly to a point. These features are shown on the well-preserved material from Thailand. A pygidium in our collections shows fewer axial and pleural segments, but is larger than Lu's (1975, pl. 30, figs 11–12) specimens, which resemble transitory pygidia in having several 'unreleased' segments anteriorly. Lu discussed differences from other *Cyclopyge* species; in view of their pelagic habits it seems plausible that critical revision will show some species to be more widely distributed than is recognized by the current taxonomy.

Genus MICROPARIA Hawle and Corda, 1847

Type species. Microparia speciosa Hawle and Corda, 1847, Ashgill (Kralův Dvůr Formation), Bohemia, by monotypy.

Microparia cf. *speciosa* Hawle and Corda, 1847

Plate 4, figures 6, 8–9

Material. Cranidium, It 25875; pygidium, It 25876.

Stratigraphical range. Upper part of Pa Kae Formation section, 18–42 m above base.

Remarks. Microparia species are difficult to determine without well-preserved, entire specimens. Material from Thailand includes cranidia which are dorsally quite featureless, and are approximately as wide (tr.) as long in dorsal view. The truncate front of the cranidium indicates that the eyes were separated in this species, rather than fused anteriorly. Marek (1960) stated that the cranidium of *M. speciosa* is narrower than long, but his illustration (text-fig. 11) is equidimensional. Pygidia from Thailand have a depressed border which is most conspicuous posterolaterally, much like that of *M. speciosa* from Bohemia. Tripp *et al.* (1989) stated that *M. adnascenta* Ju (*in* Qiu *et al.*, 1983) from the Ashgill of China differs from *M. speciosa* only in its longer pygidium; the Thai material is like *M. speciosa* in this regard. Generally similar pygidia from Langkawi were described by Kobayashi and Hamada (1978) as *M.* cf. *speciosa*, but their plate 2, figure 8*a* shows a dense sculpture of terrace lines. The species *M. sagaviaformis* Kobayashi and Hamada, 1970, from Malaysia, is certainly different, having a well-defined pygidial axis and prominent border. Because I have not assigned free cheeks, and the Thai material is stratigraphically older than the type material of *speciosa*, I have qualified the determination.

Genus LONCHODOMAS Angelin, 1854

Type species. Ampyx rostratus Sars, 1835, Vollen Formation, Oslo, Norway.

Lonchodomas jiantsaokouensis Lu, 1975

Plate 4, figures 7, 13

1975 *Lonchodomas jiantsaokouensis* Lu, p. 421, pl. 41, figs 11–12.

Material. Incomplete cranidia, It 25456, 25907; pygidia, It 25457–25458.

Stratigraphical range. Middle part of Pa Kae Formation, 14·4–18·0 m from base.

Remarks. Lu (1975) described this species fully from the upper Caradoc of Guizhou Province. Ji (1986) listed it from the Pagoda Limestone Formation in Sichuan and Shaanxi provinces. Material from Thailand is fragmentary, but well preserved. A cranidial fragment does not show the frontal spine, but does show very well the wide, low and gently concave-sided glabella which the holotype (Lu 1975, pl. 41, fig. 12) also displays. Neither of Lu's figured specimens shows the occipital ring as clearly as does the Thai specimen; it is unusual in that it runs directly and without a break into the posterior borders. Pygidium more than twice as wide as long, with a deep border; apart from an anterior pair of pleural furrows the pleural fields lack clear segmentation. Baldis and Pothe de Baldis (1995) erected *Raphioampyx*, type species *R. argentinus*, from Precordillera, Argentina, which appears to display exactly the same strange border + occipital structure as shown on the Pa Kae material, and it may prove that *jiantsaokouensis* should be accommodated in this genus.

EXPLANATION OF PLATE 4

Figs 1–5. *Cyclopyge recurva* Lu, 1962. 1–2, It 25871; well-preserved cranidium, dorsal and anterior views; × 9. 3, 5, It 25872; cranidium in lateral and anterior views; × 12. 4, It 25873; pygidium; × 12. All 42 m.

Figs 6, 8–9. *Microparia* cf. *speciosa* (Hawle and Corda, 1847). 6, 9, It 25875; cranidium in dorsal, × 10, and anterior views, × 12. 8, It 25876; pygidium; × 9. Both 42 m.

Figs 7, 13. *Lonchodomas jiantsaokouensis* Lu, 1975. 7, It 25456; incomplete cranidium; × 8. 13, It 25458; pygidium; × 8. Both 14·4 m.

Figs 10–11. *Lonchodomas rhombeus* Kobayashi and Hamada, 1978; It 25192; incomplete cranidium in dorsal and lateral views; 10·4 m; × 10.

Figs 12, 14–15. *Taklamakania* sp. indet. 12, 15, It 25500; incomplete cranidium, oblique lateral and dorsal views; × 15. 14, It 25499; small incomplete cranidium; × 15. Both 0·6 m.

Specimen details as for Plate 1, figures 1, 3–12.

PLATE 4


1


2

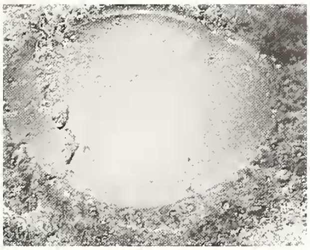

3


4


5


6


7


8


9

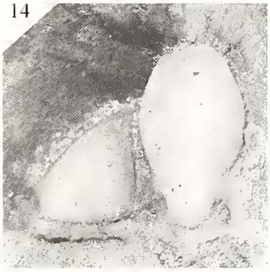

10


11

12

13

14



15

FORTEY, Ordovician trilobites

Lonchodomas rhombeus Kobayashi and Hamada, 1978

Plate 4, figures 10–11

1978 *Lonchodomas rhombeus* Kobayashi and Hamada, p. 22, pl. 2, fig. 12*a*–*b*.

Material. Cranidium, It 25192, plus unnumbered fragment.

Stratigraphical range. Pa Kae Formation, 10·4–37·0 m above base.

Remarks. A Thai cranidium is identical to the holotype of *L. rhombeus* from Langkawi Island. The rhombic glabella with a feeble median carination were deemed characteristic of the species by the original authors. However, they did not compare it with material from China described by Lu (1975), which includes several species of *Lonchodomas* with rhombic glabellas. The closely similar *L. yohi* probably has a narrower posterior border. *L. nanus* Zhou, 1982, from the Chedao Formation, Gansu Province (see also Zhou and Dean 1986, pl. 63, figs 8–9, 11, 13), is apparently indistinguishable, and may prove to be a junior synonym.

Genus TAKLAMAKANIA Zhang, 1979

Type species. Taklamakania tarimensis Zhang, upper Ordovician Engan Formation, Xinjiang Province, China, by original designation.

Taklamakania? sp. indet.

Plate 4, figures 12, 14–15

Material. Cranidia, It 25499–25500.

Stratigraphical range. Low in the Pa Kae Formation section, 0·6 m above base.

Remarks. Two small cranidia can be compared to that of the type species of *Taklamakania*, *T. tarimensis*, and to *Taklamakania* sp. from the Tangtou Formation described by Tripp *et al.* (1989). However, because *Taklamakania* is typified by having only three thoracic segments, and there is no articulated material from Thailand, the identification to genus is necessarily cautious. However, the cranidium shows a short frontal spine with a rhomboidal cross section, convex fixed cheeks and a distinct forward curve of the posterior border furrow laterally. All these features seem to be typical of previously figured *Taklamakania* cranidia, and are unlike, for example, *Ampyx*. The Thai specimens differ from previously described Chinese cranidia in that the alae are hardly developed, and the lateral border widens laterally only slightly. There is insufficient material to consider erecting a new species.

Family PROETIDAE Salter, 1864

Genus PARVIGENA Owens, 1973*a*

Type species. Proetus parvigenus Warburg, 1925, from the Boda Limestone (Ashgill) Sweden, by original designation.

Remarks. Owens (1973*a*) regarded this effaced genus as difficult to place within the proetoids, where such a high degree of effacement is uncommon. A species from Thailand helps to clarify relationships, because it is less effaced. *P. plana* (Zhou and Xiang, 1993) was placed in *Stenoblepharum* Owens by the original authors, but I believe it shows several derived characters that link it with *Parvigena*. First, there is an effacement of the cranidial border (an uncommon feature in proetids), producing a convex slope in front of the glabella. This is well shown on Plate 5, figure 1, and by Zhou and Xiang's (1993) plate 1, figure 13, while other specimens from the Pagoda Limestone show a faint remnant of the border. The free cheek is narrow (Pl. 5, fig. 2) and the lateral border is also effaced – but not the posterior border – a feature that can be matched exactly on *Parvigena* (Owens 1973*a*, fig. 14M). The only substantial difference on the slightly younger Swedish species is that effacement has proceeded further such that the front of the glabella is obscure. If this interpretation is correct then *Parvigena* is an effaced proetid. Its closest relatives may lie with a species currently classified in *Stenoblepharum*, as Zhou and Xiang (1993) implied.

Parvigena plana (Zhou and Xiang, 1993)

Plate 5, figures 1–3, 5

1993 *Stenoblepharum planum* Zhou and Xiang, p. 58, pl. 1, figs 12–16; pl. 2, figs 1–7.

Material. Cranidia, It 25370, 25372, 25374; free cheek, It 25371.

Stratigraphical range. Higher part of Pa Kae Formation section, 39 m above base.

Revised diagnosis. *Parvigena* having the front of the glabella defined, and wider cheeks than *P. parvigena*; surface sculpture of fine lines.

Remarks. Zhou and Xiang (1993) provided a full description. The resemblance between Chinese and Thai material is almost complete; the effacement of the cephalic border on the new material is possibly greater, and a faint, relict cranidial border is present on most of the Pagoda Limestone material illustrated. However, Zhou and Xiang's plate 1, figure 13 is identical to the Pa Kae specimens in this feature. The Thai material also shows the surface sculpture well, but it is clear from the description that the same 'lined' sculpture is present on the Pagoda Limestone specimens. There are no taxonomic grounds for separating the new material from that from China.

Genus HANJIANGASPIS Zhou and Xiang, 1993

Type species. *Harpidella (s.l.) fibrisulcatus* Ji, 1986, from the Pagoda Limestone of Liangshan, Nanzheng, by original designation.

Hanjiangaspis fibrisulcata (Ji, 1986)

Plate 5, figures 10–13

1986 *Harpidella (s.l.) fibrisulcatus* Ji, p. 19, pl. 4, fig. 12.
1993 *Hanjiangaspis fibrisulcatus* (Ji); Zhou and Zhang, p. 61, pl. 2, figs 8–16.

Material. Cranidia, It 25250, 25368, 25421; free cheeks, It 25251, 25289.

Stratigraphical range. Upper part of Pa Kae Formation section, 24–42 m above base.

Remarks. This distinctive species was given a perfunctory description by Ji (1986) and a much fuller one by Zhou and Xiang (1993), who illustrated good material. I cannot add anything new here. The strange elongate glabella, which is concave-sided, the lack of incised glabellar furrows, and the coarse granulate surface sculpture are all distinctive features shared between Thai and Pagoda Limestone specimens. Zhou and Xiang allowed some variation in the preglabellar field in the species; the Thai specimens compare exactly with their plate 2, figure 8*a* in that little of the preglabellar field is visible in dorsal views. Other specimens from the Pagoda Limestone seem to have a longer (sag.) preglabellar field, but this is accepted as variation within the population of the type species. Despite some resemblance to a dimeropygid, the pygidium attributed to the genus by Zhou and Xiang clearly shows proetid affinities.

Family RORRINGTONIIDAE Owens, *in* Owens and Hammann, 1990

Genus RORRINGTONIA Whittard, 1966

Type species. *Rorringtonia flabelliformis* Whittard, 1966, lower Caradoc, Shropshire, by original designation.

Remarks. Owens (*in* Owens and Hammann, 1990, p. 240) diagnosed the family Rorringtoniidae to include a number of aulacopleuroid genera with three pairs of glabellar furrows. The eyes are somewhat removed from the glabella, unlike in Proetidae in which the palpebral lobes lie adjacent to the axial furrows. However, this is a plesiomorphic feature, as are the features given in Owens' (*in* Owens and Hammann 1990) diagnosis of the family. Whittard's original material of *Rorringtonia* was flattened but Owens (1973*b*, pl. 15, fig. 9) illustrated some better preserved material of *R. vetula* (Reed) from the Scottish Caradoc. On this species, the basal glabellar furrows curve backwards towards the occipital ring but become effaced posteriorly. The same feature is shown by the type species of *Chenaspis*, *C. lepida*, from the Pagoda Limestone (Zhou and Xiang 1993); indeed, cranidia of this species are hardly distinguishable from that of *Rorringtonia vetula*. The distinguishing characters of *Chenaspis* from *Rorringtonia* given by Zhou and Xiang include downsloping preglabellar field and 'S1 shorter and far from occipital furrow posteriorly'. The downsloping preglabellar field is probably a function of different preservation, since the Chinese specimens are preserved in full relief, and Whittard's material of the type species was flattened. The shorter S1 is just a matter of where the effacement begins; Zhou and Xiang's plate 3, figure 2 clearly shows the continuation of S1 posteriorly. Neither of these characters is persuasive as a generic differential and I believe *Chenaspis* can be incorporated within *Rorringtonia*. *Trigonoproetus* Apollonov, 1974, of which the type species was described from three cranidia from the upper Ordovician of Kazakhstan, was not listed as a rorringtoniid by Owens (*in* Owens and Hammann 1990). The position of its eye is ambiguous from the specimens illustrated, but in other respects it appears to be identical to *Chenaspis*, and thus to *Rorringtonia*. *Rorringtonia lenis* Owens and Hammann, 1990, from the upper Ordovician of Spain, is a species with a wider cranidial border and shorter preglabellar field; this further extends the range of morphology within *Rorringtonia*.

EXPLANATION OF PLATE 5

Figs 1–3, 5. *Parvigena plana* (Zhou and Xiang, 1993). 1, 5, It 25370; 1, cranidium; × 15; 5, detail, × 30. 2, It 25371; free cheek, dorsal view; × 12. 3, It 25372; cranidium; × 12. All 39 m.

Figs 4, 7–8. *Rorringtonia* cf. *lepida* (Zhou and Xiang, 1993). 4, It 25373; large cranidium; × 15. 7, It 25361; small cranidium; × 20. 8, It 25360; pygidium; × 20. All 39 m.

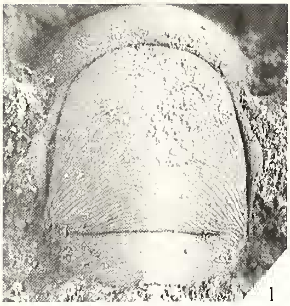
Figs 6, 9. *Cyamella* sp. 1; It 25455. 6, cranidium; 14·4 m; × 15. 9, anterior view; × 10.

Figs 10–13. *Hanjiangaspis fibrisulcata* (Ji, 1986). 10–11, It 25368; cranidium in lateral and dorsal views; 39 m; × 15. 12–13, It 25250; cranidium in dorsal and anterior views; 42 m; × 10.

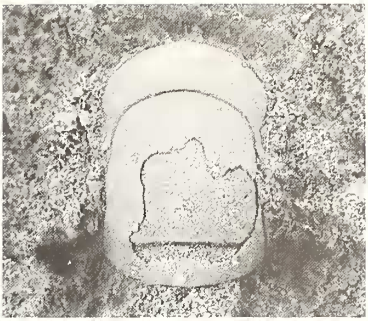
Figs 14–15. *Phaseolops*? cf. *conus* (Hu, 1971); It 25454; 14·4 m. 14, incomplete cranidium; × 12. 15, anterior view; × 9.

Figs 16–17. *Telephina convexa* Lu, 1975; It 25877; cranidium in dorsal and anterior views; 18 m; × 8.

Specimen details as for Plate 1, figures 1, 3–12.


1

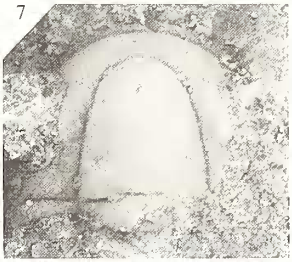

2


3


4


5


6

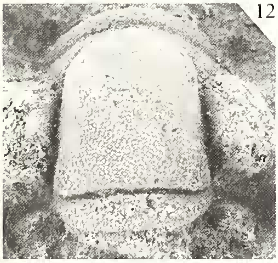

7

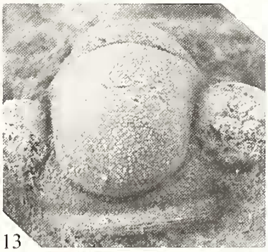

8


9


10


11

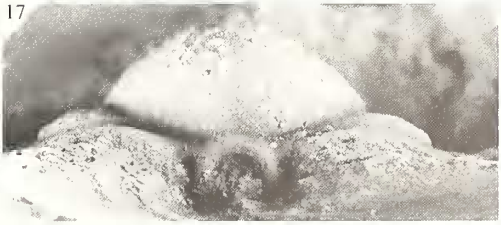

12


13


14


15


16


17

FORTEY, *Ordovician trilobites*

Rorringtonia cf. *lepida* (Zhou and Xiang, 1993)

Plate 5, figures 4, 7–8

Material. Cranidia, It 25294, 25361, 25373; pygidia, It 25316, 25360.

Stratigraphical range. Pa Kae Formation section, 10·4–39 m above base.

Remarks. The larger cranidium clearly shows the form of the 1S glabellar furrow, which is shallow anterolaterally, deepens, and then shallows again as it turns to the posterior to meet the occipital furrow. This is true also of *R. lepida*, as it is of the type species of *Trigonoproetus*, *T. triquetus*. The holotype of this species (Apollonov 1974, pl. 19, fig. 1) has a less tapering glabella than *R.* cf. *lepida* but another specimen (Apollonov, pl. 19, fig. 2) is identical in glabellar shape. The occipital ring appears to be narrower (exsag.) on the Thai specimen, but a very prominent occipital tubercle is present. The only difference from *R. lepida* (Zhou and Xiang, 1993) from the Pagoda Limestone is that it shows a more equal development of the three pairs of glabellar furrows, and has a sharply elevated anterior cranidial border. *R. vetula* (Reed, 1935) (Owens 1973*b*, pl. 15, figs 9–10) from the Caradoc Balclatchie Group, Scotland, is also closely similar, and differs from the Thai specimen only in its longer incised portion of 1S. A well-preserved, but small pygidium from Thailand has a longer postaxial field than does the pygidium attributed to *R. lepida* (Zhou and Xiang 1993, pl. 3, fig. 3).Without more material the significance of these small differences cannot be assessed, and a provisional determination is given.

Genus CYAMELLA Owens *in* Owens and Hammann, 1990

Type species. Cyamops stensioei, upper Ordovician, Sweden, original designation.

Remarks. Cyamella was proposed by Owens (*in* Owens and Hammann 1990) as a replacement name for *Cyamops*, Owens, 1979, which was preoccupied. Two species were assigned to the genus by Owens (1979) of which one, the late Caradoc *Cyamella* sp. 1, is comparatively effaced, with ill-defined cranidial border furrow compared with the type species. Zhou and Xiang (1993) erected *Paracyamella* for two similarly effaced species from the Pagoda Limestone Formation. Apart from effacement, these authors cited 'weakly divergent anterior branches of the facial sutures' and 'medially placed and long palpebral lobe' as differences between *Paracyamella* and *Cyamella* recognizable from the cranidium. However, comparing *Cyamella* sp. 1 with *Paracyamella hujiabaensis* figured by Zhou and Xiang (1993, pl. 4, fig. 1) there is no difference in the divergence of the sutures in front of the palpebral lobes, as seen in dorsal view (> 20°), and any difference in the position of the eye between *Cyamella stensioei* and *P. hujiabaensis* is accounted for by the slightly longer palpebral lobe of the latter. The species from Thailand is effaced like *Paracyamella* but with the palpebral lobe like *Cyamella stensioei*. Hence the differences between the genera are both slight and intergradational, and I prefer to regard *Cyamella* as the senior synonym.

Cyamella sp. 1

Plate 5, figures 6, 9

Material. Cranidium, It 25455.

Stratigraphical range. Pa Kae Formation section, 14·4 m above base.

Description. The well-preserved cranidium has a weakly tapering glabella with a truncate front, which shows only the faintest indications of lateral glabellar furrows of rorringtoniid form. The occipital furrow is better defined; the occipital ring has a median tubercle. The preglabellar field slopes downwards to a rather ill-defined, almost concave, border. Anterior branches of the facial suture diverge at about 30° to the sagittal line as seen in dorsal view. Palpebral lobes are one-third length of glabella (sag.).

Remarks. The poorly defined anterior cranidial border and the truncate glabella are the most obvious differences from *C. stensioei.* The closest species is *C. hujiabaensis*, from the Pagoda Limestone Formation (especially Zhou and Xiang 1993, pl. 4, fig. 1), which, however, has an evenly parabolic glabellar outline, and less divergent anterior branches of the facial sutures. The glabella outline resembles that of some *Rorringtonia* species, e.g. *R. lenis* Owens and Hammann, 1990. There is not enough material to name this species formally.

Genus PHASEOLOPS Whittington, 1963

Type species. Phaseolops sepositus Whittington, Cow Head Group (middle Ordovician), western Newfoundland, by original designation.

Phaseolops? cf. *conus* Hu, 1971

Plate 5, figures 14–15

Material. Cranidium, It 25454.

Stratigraphical range. Block from lower part of Pa Kae section, not precisely localized.

Remarks. A single specimen is compared to a species described from silicified specimens by Hu (1971, p. 111) as *Phaseolops conus* from the Edinburg Formation of Virginia. I doubt whether Hu was correct in referring this species to *Phaseolops.* Whittington's type species has a well-developed S2, as well as palpebral lobes placed close to the glabella in proetid fashion. *P. conus*, on the other hand, has a weak S2, and palpebral lobes with distinct rims, and well removed from glabella in rorringtoniid fashion. The Thai species is very like that from the Edinburg Formation, apart from having a narrower cranidial border. It even shows an unusual sculpture of scattered tubercles on the preglabellar field, which is also present on the American species. This is the one connection with faunas outside Gondwana, but a single specimen is not adequate for a reconsideration of *P. conus*. Here I place the species in Rorringtoniidae, and simply compare it with Hu's species.

Family TELEPHINIDAE Marek, 1952

Genus TELEPHINA Marek, 1952

Type species. Telephus fractus Barrande, 1852, Ashgill, Bohemia, by original designation.

Telephina convexa Lu, 1975

Plate 5, figures 16–17; Text-figure 3

Synonymy. See Tripp *et al.* 1989, p. 44.

Stratigraphical range. Upper part of the Pa Kae Formation section, 14·4–42 m above base.

Material. Cranidia, It 25272, 25877; free cheeks, It 25269–70, 25429.

Remarks. The description of the type material by Lu (1975) mentioned only cranidia, but Tripp *et al.* (1989) assigned a free cheek and pygidium. The well-preserved cranidium from the Pa Kae Formation illustrated here is exactly like Lu's holotype, but shows the small, near vertical occipital spine developed near the back end of the occipital ring which Tripp *et al.* (1989) recorded on material form the Tangtou Formation. Also typical of the species is very coarse tuberculation which does not extend on to the muscle insertion areas, in which the best Thai specimen matches the holotype and that illustrated by Lu and Zhou (1981, pl. 6, fig. 8); sculpture is weakly reflected on internal moulds. The glabellar muscle impressions are clearly shown; it should be noted that the bulk of the fixigenal field is another such area, so that the tuberculate sculpture is confined to its perimeter. A species described by Weir (1959) as *Telephina* cf. *reedi* from the Ashgill of Co. Clare, Ireland, has apparently similar sculpture; the rectangular shape of the glabella of the material illustrated is certainly the product of tectonic distortion. I have prepared the anterior cranidial border of the Thai cranidium, which is curved into an inverted 'U' (Pl. 5, fig. 17). A species described as *Telephina hangzhongensis* from the Pagoda Limestone by Chen (*in* Li *et al.* 1975) shows a similar border and sculpture, and may be a synonym of *T. convexa*. The pygidium associated with this species (Chen *in* Li *et al.* 1975, pl. 19, fig. 2*a*–*b*) is assuredly not that of a *Telephina*, being both too convex (tr.) and having too many pleural segments. The reconstruction of *Telephina spinifera* given in the *Treatise* (Whittington *in* Moore 1959, p. 298) is incorrect in portraying the border as a pair of anteriorly directed spines. The two large glabellar muscle impressions may indicate that the number of cephalic limbs was reduced in *Telephina*, possibly in connection with its pelagic mode of life.

The square-lensed eyes (Text-fig. 3) are described above. Tripp *et al.* (1989) made no mention of anything unusual about the eye lenses. The immature cheek illustrated on their figure 9*u* seems to show polygonal lenses, and very few files dorsoventrally, and so it may be the case that in earlier instars the eye was of a more conventional holochroal type. At intermediate size the Thai material shows at least 25 lenses counting along an obliquely arranged row of 'squares' from bottom to top of the eye. Ji (1986) recorded *T. convexa* from the Pagoda Limestone, and, although the type material is from the slightly younger Linhsiang Formation (early Ashgill; see Chen *et al.* 1995), the similarity between type material and the new collections from Thailand indicates their conspecificity.

Family PHILLIPSINELLIDAE Whittington, 1950

Remarks. Xia (1978, p. 176) erected a family Quyuaniaidae [*sic*] based on the monotypic genus *Quyuania*, which was erected in the same paper. I regard this genus as a phillipsinellid and, if this view is correct, a separate family is redundant.

Genus PARAPHILLIPSINELLA Lu, *in* Lu and Chang, 1974

Type species. Paraphillipsinella globosa Lu, *in* Lu and Chang, 1974, Pagoda Formation (Caradoc), Sichuan, China, by original designation.

EXPLANATION OF PLATE 6

Figs 1, 3–5, 9. *Paraphillipsinella globosa* Lu, 1974. 1, 3, 5, It 25879; cephalic shield in anterior, lateral and dorsal views; 18 m; × 15. 4, It 25880; cephalic shield with frontal lobe of glabella broken off, showing eyes; 18 m; × 13. 9, It 25881; incomplete cranidium; 0·6 m; × 12.

Figs 2, 10. *Paraphillipsinella nanjiangensis* Lu, 1974. 2, It 25323; cast from mould of small cephalic shield; 41 m; × 12; 10, It 25353; cranidium; 39 m; × 18.

Fig. 6. *Quyuania* cf. *ziguiensis* Xia, 1978; It 25453; cranidium; 14·4 m; × 9.

Figs 7–8, 11–12, 15. *Cekovia transversa* (Ji, *in* Sheng and Ji, 1987). 7, It 25444; small cranidium; 18 m; × 10. 8, It 25288; larger pygidium with doublure; 18 m; × 5. 11, It 25326; pygidium; 18 m; × 10. 12, 15, It 25279; cranidium, dorsal and anterior views; 24 m; × 4.

Figs 13–14, *Cekovia striata* Ji, 1986. 13, It 25382; larger pygidium, incomplete on right hand side; 37 m; × 8. 14, It 25882; transitory pygidium retaining one unreleased segment; 18 m; × 10.

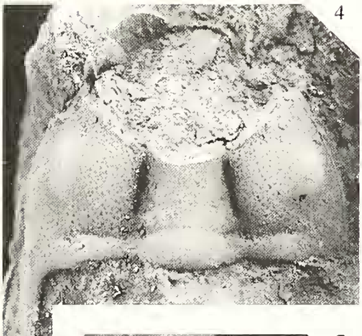
Specimen details as for Plate 1, figures 1, 3–12.

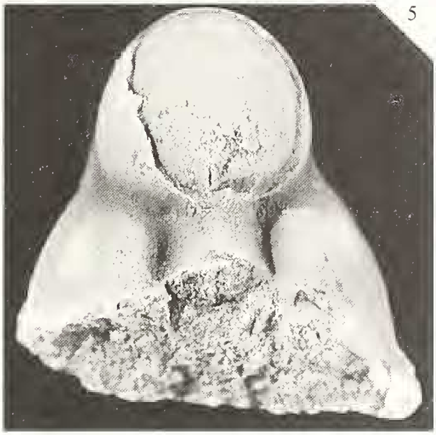
PLATE 6


1


2


3


4

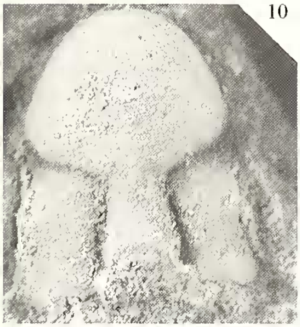

5


6


7


8


9


10


11


12


13


14


15

FORTEY, Ordovician trilobites

Paraphillipsinella nanjiangensis Lu, 1974

Plate 6, figures 2, 10

Synonymy. See Tripp *et al.* 1989, p. 43.

Material. Cephalic shields and cranidia, It 25246–25249, 25323, 25353, 25356*a–b*.

Horizon. Upper part of Pa Kae Formation section, 37–42 m above base.

Remarks. There is uncertainty about how many species of *Paraphillipsinella* may be recognized. Rather a large number has now been described from the Yangtze region of southern China, but their range of variation is unclear. A complete exoskeleton was figured by Qiu *et al.* (1983, pl. 76, fig. 9), but there is only cephalic material from Thailand. Ji (1982) reviewed the genus and gave some measurable parameters with which to distinguish up to seven species. Lu and Zhou (1981) recognized only two species: *P. globosa* Lu, *in* Lu and Chang, 1974, with a sub-circular frontal glabellar lobe, and *P. nanjiangensis* Lu, *in* Lu and Chang, 1974, with a more transversely oval frontal lobe. The Thai species illustrated in Plate 6, figure 2 is clearly different from *P. globosa* (Lu *in* Lu and Chang 1974, pl. 53, figs 8–9; Zhou and Dean 1986, pl. 62, figs 13–16), and more like *P. nanjiangensis* with regard to the frontal glabellar lobe. Ji (1982, fig. 2) recognized *P. nanjiangensis* as the stratigraphically earlier part of a lineage ranging through the Pagoda Limestone and comprising this species and *P. funga* Ji, 1982. However, because Tripp *et al.* (1989) recognized *P. nanjiangensis* from the formation above the Pagoda Limestone the stratigraphical difference is unlikely to apply. The choice of assignment of the Thai species is between these two species, if indeed they are distinct. The ratio of maximum to minimum glabella width given in Ji's (1982, p. 60) chart appeared to provide a distinction between *nanjiangensis* and *funga*, the latter being relatively broader. However, the ratio in well-preserved Thai material spans the range (2·9 to 3·5) for the two species. I think it likely that these two taxa are just part of a single variable species. Tripp *et al.* (1989) thought that *funga* might have a less inflated glabella, a difference I find hard to apply given the range in preservation styles of the material illustrated in previous works. Accordingly, I use *P. nanjiangensis* here. The cephalic material from Thailand is beautifully preserved; one specimen (Pl. 6, fig. 2) retains the free cheek showing the indistinct eye lobe and short genal spine.

Paraphillipsinella globosa Lu, *in* Lu and Chang, 1974

Plate 6, figures 1, 3–5, 9

Synonymy. See Zhou and Dean (1986, p. 767).

Material. Cephalic shields, It 25879–25880; cranidia, It 25451–25452, 25496–25497, 25881, 25903–25906; pygidia, It 25498, 25908–25909.

Stratigraphical range. Lower to middle part of Pa Kae Formation, 0·6–18 m above base.

Remarks. This species has been described several times, most recently in English by Zhou and Dean (1986), who itemized several synonyms in the Chinese literature. The almost perfectly spherical frontal glabellar lobe immediately differentiates this species from *P. nanjiangensis*. The small, nearly entire cephalic shield illustrated here is probably the best preserved specimen known. It shows the eye surface very well, but even using high magnification I have been unable to see any lenses (which are commonly seen on other Thai species) and I presume they were minute. The venter bulges downwards (Pl. 6, fig. 3) so that the frontal glabellar lobe is essentially a sphere; raised lines on the genal border pass on to the frontal lobe where they split into anastomosing lines, and ventrally there are strong cuesta-like terrace ridges of which the scarp slopes face anteriorly.

Genus QUYUANIA Xia, 1978

Type species. Quyuania ziguiensis Xia, 1978, Pagoda Limestone, by original designation.

Remarks. Although accommodated in a separate family by Xia (1978), the type species of *Quyuania* appears similar to some species of the *matutina* species group which have been assigned to *Phillipsinella* (Bruton 1976, p. 707), for example *P. fornebuensis* Bruton, 1976, from the Caradoc of Norway. In comparison with *Phillipsinella parabola*, these species have a relatively unexpanded (tr.) frontal glabellar lobe. *Quyuania* may be retained for those species in which the maximum transverse glabellar width is less than twice the minimum width of the glabella behind, and which have an occipital ring which is not unusually long (sag.). Tripp (1962) established a genus, *Kirkdomina*, on the basis of small specimens of the type species, *K. williamsi*, from the *Confinis* Flags (Llanvirn) of the Girvan District, Scotland. It is similar to *Quyuania* apart from in its narrow (tr.) anterior cranidial border, but I am uncertain whether the similarity is significant in view of the immaturity of Tripp's specimens.

Quyuania cf. *ziguiensis* Xia, 1978

Plate 6, figure 6

Material. Cranidium, It 25453.

Occurrence. Pa Kae Formation section, 14·4 m above base.

Remarks. Q. ziguiensis from the Pagoda Formation has been figured by Xia (1978), Ji (1986) and Sheng and Ji (1987), and has a distinctive sculpture, comprising bowed, elevated lines on the glabellar frontal lobe, which can be matched on the Thai cranidium. However, the frontal glabellar lobe is even less inflated on the latter, and the cranidial border may also be wider. If it is a different species, the specimen is not an adequate basis for naming it formally.

Family ILLAENIDAE Hawle and Corda, 1847

Genus CEKOVIA Šnajdr, 1956

Type species. Illaenus transfuga Barrande, 1852, Caradoc, Bohemia, by original designation.

Remarks. The differences between certain species of *Parillaenus* and those of *Cekovia* are not great. For example, *Parillaenus dalecarlicus* (Warburg, 1925) was redescribed by Bruton and Owen (1988), and has a comparatively well-defined, waisted glabella, unlike the type species, *P. fallax* Holm, but like some *Cekovia* species. The species from Thailand has a similar glabellar shape. Since this is likely to be a plesiomorphic (styginid-form) character, its significance in generic diagnosis is unclear. However, a well-defined pygidial axis seems to be more characteristic of *Cekovia* than of typical illaenids. Hammann (1992, p. 62) cited the Pagoda species *C. striata* Ji, 1986, as a typical *Cekovia* and the species described below is referred to the same genus.

**Cekovia transversa* (Ji, *in* Sheng and Ji, 1987)

Plate 6, figures 7–8, 11–12, 15

1987 *Illaenus transversus* Ji, *in* Sheng and Ji, p. 30, pl. 1, figs 1–2.

Material. Cranidia, It 25279, 25440, 25444; pygidia, It 25288, 25326, 25487.

Stratigraphical range. Pa Kae Formation section, 0·6–24 m above base.

*See note on p. 449.

Description. The material from Thailand is rather better preserved than the specimens from the Pagoda Limestone used by Ji to found *Illaenus transversus*, and such differences as there are may be no more than preservational. On Thai material, the cranidium is moderately convex, and the glabella is distinctly waisted at one-quarter to one-third cranidial length in dorsal view. At its narrowest, the glabella is half the cranidial length. The smaller cranidium shows a well-marked occipital tubercle. Palpebral lobes are large for the genus, approximately one-third cranidial length, but I cannot be certain of this feature on Ji's material. Surface sculpture of terrace ridges on the anterior part of the cranidium where the axial furrows are obsolete.

Distinctive pygidium with length/width ratio ranges from 0·4 to 0·6, and the axis occupies one-quarter of the transverse width, and about one-third the length. The axis is wider than long with an acutely triangular outline. Two narrow and obscurely defined axial rings are visible on smaller specimens, but not on larger ones. There is a faint median postaxial ridge. There is a pair of outwardly diverging furrows running across the pleural fields from the mid length of axial furrows; these extend as far as the paradoublural line, and may represent its adaxial continuation. The doublure on the largest pygidium proved difficult to prepare, but certainly widens mesially (Pl. 6, fig. 8).

Remarks. Despite its distinctive pygidium, this is a difficult species to name with certainty. Ji (*in* Sheng and Ji 1987) illustrated a cranidium and pygidium, rather indistinctly. However, the pygidium shows the outward curving furrows crossing the adaxial parts of the pleural fields which are a distinctive feature of the species. Ji's specimens are larger than the Pa Kae specimens, which may account for their wider cephalic and pygidial axes. However, it would be difficult to apply a different name in view of the similarity of the pygidia, given the identity of other Thai species to those from the Pagoda Formation. It is unclear whether Ji's designation is valid, because there is no formal description, apart from the legend to the figure. The Chinese cranidium illustrated is very much larger than any discovered from the Pa Kae Formation, which may account for its greater effacement and smaller eyes. Other details are uncertain because of the poor illustration. The Thai cranidium is very like that attributed by Ji (1986) to *Cekovia striata* from the Pagoda Limestone Formation; however, the pygidium assigned to that species lacks the characteristic dorsal furrows, and is longer (sag.). I have assigned the cranidia figured here to *transversa* because they are associated in one bed in similar abundance.

Cekovia striata Ji, 1986

Plate 6, figures 13–14

Material. Pygidia, It 25382, 25882–25883; ?cranidium, It 25383.

Stratigraphical range. Upper part of Pa Kae Formation section, 18–42 m above base.

Remarks. Pygidia differ from those attributed to *C. transversa* in lacking the distinctive dorsal furrows of that species, and in having a more concave-sided pygidial axis. Similar differences apply to *C. striata*, to which the Thai species is assigned. An immature pygidium figured herein is similar to that assigned by Ji (1986, pl. 3, fig. 12) to *Cekovia striata* in showing a post-axial ridge.

Family PANDERIIDAE Bruton, 1968

Genus PANDERIA Volborth, 1863

Type species. Panderia triquetra Volborth, 1863, lower middle Ordovician of St Petersburg, by monotypy.

Panderia orbiculata Ji, 1986

Plate 7, figures 1–6

1986 *Panderia orbiculata* Ji, p. 17, pl. 4, figs 3–6.
1987 *Panderia orbiculata* Ji; Ji, *in* Sheng and Ji, pl. 1, fig. 18.

Material. Cephala, It 25307–25308; cranidia, It 25309, 25235–25236; pygidia, It 25233, 25411, 25428; cheeks and genal doublure, It 25237, 25306.

Stratigraphical range. Upper part of Pa Kae Formation section, 18–42 m above base.

Description. Ji's short description of *P. orbiculata* from the Pagoda Limestone is supplemented here. *P. orbiculata* belongs within a section of *Panderia* with comparatively well-defined axial furrows; Ji's specimens are exfoliated, but furrows are also distinct on the material from Thailand, which retains its cuticle. Bruton (1968, p. 2) has pointed out that illustrations of *Panderia* cranidia vary greatly according to how the specimens are oriented. Dorsal and palpebral views are used here according to Bruton's definition. In palpebral view, the cephalon is two-thirds as long as wide. In dorsal and palpebral views the axial furrows diverge outwards-forwards, converging anteriorly. Glabella distinctly convex (tr.); in the best-preserved specimen the anterior part is steeply downsloping and the posterior is close to horizontal, and there is a rather sharp break in slope between these two parts, producing a blunt point on the profile (Pl. 7, fig. 3). The same specimen shows a pair of prominent muscle insertion areas opposite the posterior part of the eye, and two small and faint pairs behind. Eyes approach half cephalic length in palpebral view; in lateral view the eye is about three times as long as high. Eye lenses are exceedingly small and numerous. Free cheeks are very narrow (tr.), without border. The distance from the front of the eye to the anterior cephalic margin is short, and the anterior section of the facial suture reflects this. A pygidium (Pl. 7, fig. 5) is typical of the genus and is probably correctly associated. The axis is well defined for the genus, and the doublure outline is parallel to the posterior pygidial margin.

Remarks. This species is very like an Ashgill species from Norway, *P. insulana* Bruton, 1968, which also has the eye extending far forwards. It differs from this, and other *Panderia* species, in the low downward curvature of the posterior part of the glabella, such that in dorsal view the cranidium is relatively long (sag.). The eye is proportionately deeper in *P. orbiculata*; on *P. insulana* the visual surface is at least four times longer than deep. Although the Thai material is better preserved than that illustrated by Ji (1986, pl. 4, fig. 6), the cranidium of the specimen illustrated on Plate 7, figure 6 is identical, and it seems very likely that it is the same species. The poorly illustrated *Panderia* sp. of Apollonov (1974) from the upper Ordovician of Kazakhstan may prove to be the same species.

Panderia migratoria Bruton, 1968

Plate 7, figures 7–14

Material. Cephala, It 25854–25855, 25857; cranidia, It 25180, 25563–25566, 26202; pygidia, It 25345, 25856, 25866; free cheek, It 25562.

Stratigraphical range. Lower part of Pa Kae Formation section, 0·6–39 m above base.

Remarks. Bruton (1968) gave a full description of this species from Caradoc occurrences in Norway and Sweden. It is an extremely convex form, and thus easily distinguished from *P. orbiculata*. I can find no important differences between the Thai and Scandinavian material. This is a highly effaced member of the genus, and it is possible that the Thai specimens are more so than the type series since the axial furrows are faint, even at the posterior end of the glabella, but this would scarcely be a reliable specific distinction. Of the species described by Bruton (1968) only *P. edita* is as convex, but this is a species having a long anterior branch of the facial suture.

Family STAUROCEPHALIDAE Prantl and Přibyl, 1948

Genus OEDICYBELE Whittington, 1938

Type species. O. kingi Whittington, 1938, Ashgill, North Wales, by original designation.

Remarks. The type material of the type species of *Oedicybele* Whittington, 1938 is not well preserved but Kielan (1957) figured better material from Poland, which she attributed to *O. kingi*.

This species has minute, anteriorly positioned eyes, and may be regarded as an example of an atheloptic (Fortey and Owens 1987) trilobite in which the eyes are reduced in function. *Oedicybele kildarensis* Temple, 1965 described from the Ashgill of Ireland (Temple 1965; Dean 1971), from good material, has somewhat larger, but still small, eyes. The type species of *Dindymenella* Lu (*in* Lu *et al.* 1976), *D. sulcata*, from the upper Ordovician of Yunnan, is blind, and is known from poorly preserved type material. In other features, however, it is extremely like *Oedicybele*. If I am correct in identifying the material from Thailand with the species *sulcata*, this affords a good basis for comparison with the better preserved material of *Oedicybele*. Glabellar structure is identical, not only in the presence of basal bacculae-like glabellar lobes, but also in the form of the lateral glabellar furrows, especially a shallow S4 running parallel to the axial furrow. Other details, such as the convexity of the cheeks, and even the surface sculpture, are also closely comparable. Note that the glabellar structure of the Thai species is also quite different from that of *Dindymene* and allied genera, with which *Dindymenella* might otherwise by compared on account of its blindness. The development of eyes in atheloptic trilobites is variable, and no particular taxonomic significance can be attached to the presence of relict eyes as compared with their complete absence. Thus, for example, within the dalmanitoidean genus *Ormathops* there are species with small anterior eyes and others with no eyes at all (Fortey and Owens 1987). Hence the grounds for erecting *Dindymenella* seem insufficient, and it is here considered a subjective synonym of *Oedicybele*.

Oedicybele sulcata (Lu, *in* Lu *et al.*, 1976)

Plate 10, figures 7, 10–11

Material. Cephalic shield, It 25887.

Stratigraphical range. Uppermost part of the Pa Kae Formation section, 42 m above base.

Description. Cephalon twice as wide as long in dorsal view, convex forwards. Glabella also protrudes forwards, and expands greatly over its anterior two-thirds, such that the width at the occipital ring is half that of the frontal lobe. Basal bacculae-like glabellar lobes are conspicuous, as they are in *O. kingi* (Kielan, 1957, pl. 6, fig. 3) although not shown in Kielan's reconstruction of this species. S1–S3 are short, deep, more or less transverse pit-like furrows, and S3 is continued very faintly towards the mid-line of the glabella. S4 is shallower, running close and parallel to axial furrow. Axial furrows deep, but narrow. Convex fixed cheeks show no sign of eye or facial suture. Borders widen towards genal angle where there is a short genal spine directed somewhat outwards. Narrow posterior border furrow curves round into lateral border. Dorsal cuticular surface with scattered, large tubercles, noticeable especially on glabellar frontal lobe. Genal prosopon finely reticulate.

Remarks. This species differs from *O. kildarensis* Temple in having genal spines and a finer scale reticulate sculpture on the fixed cheeks. It resembles *O. kingi* Whittington in the same features; however, in the specimen of *O. kingi* figured by Kielan (1957, pl. 5) the sculpture extends on to the glabella also. *O. kildarensis* has the largest eyes. On *O. kingi* they are much reduced, and on

---

EXPLANATION OF PLATE 7

Figs 1–6. *Panderia orbiculata* Ji, 1986. 1, 3, It 25307; cephalon, in dorsal and lateral views; 37 m; ×10. 2, 6, It 25236; cranidium, in lateral and palpebral views; 42 m; ×9. 4, It 25308; small cephalon; 37 m; ×10. 5, It 25428; pygidium; 42 m; ×7.

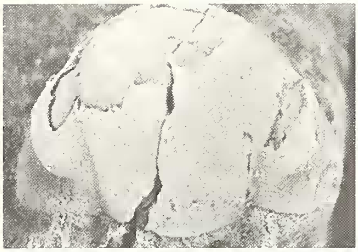
Figs 7–14. *Panderia migratoria* Bruton, 1968. 7, 10–11, It 25854; cephalon, in palpebral, lateral, and dorsal views; ×9. 8, 12, 14, It 25855; smaller cephalon in palpebral, dorsal and lateral views; ×9. 13, It 25856; pygidium; ×13. 9, It 25857; cephalon, anterior view; ×9. All 18 m.

Specimen details as for Plate 1, figures 1, 3–12.


1


2

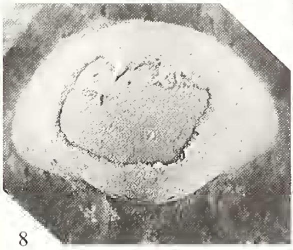

3


4


5


6


7


8

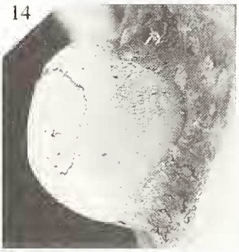

9


10


11


12


13


14

FORTEY, *Panderia*

O. sulcata they are lost altogether. Lu's original specimens are more complete but less well preserved than the Thai material, and one cannot compare sculptural details, but Lu states that the species is without eyes, and hence the closest comparison of this cephalon is with *O. sulcata* rather than *O. kingi*. A cranidial fragment from the Pagoda Limestone Formation figured by Ji (1986, pl. 6, fig. 10) as *Atractopyge*? sp. appears to be similar.

Oedicybele sp. nov. A

Plate 10, figures 8–9

Material. Cranidium, It 25477; another unnumbered cranidial fragment.

Stratigraphical range. Lower part of Pa Kae Formation section, 0·6–18 m above base.

Description. The single well-preserved cranidium is not an adequate basis on which to name what is likely to be a new species. In dorsal view the tumid glabella expands evenly forwards such that its transverse width across the frontal lobe is twice that immediately in front of the occipital ring. Glabellar furrows deep, but short. S1 transverse, showing a deep exterior part but also continues very faintly across mid-part of glabella. S2 pit-like, directed slightly forwards and inwards. S3 present only on the flanks of the glabella, a shallow pit. The frontal glabellar lobe carries large and scattered low, round tubercles. Posterior parts of fixed cheeks are strongly convex upwards. Posterior border narrow close to glabella and widening rather abruptly near genal angle. I have not succeeded in preparing the palpebral lobe although the course of the facial suture clearly shows that there were free cheeks present of about the same size as those in *O. kildarensis* (Dean 1971, pl. 17, fig. 6).

Remarks. The species from Thailand displays the same rounded and scattered glabellar tubercles as *O. kildarensis* Temple, 1965, from the Chair of Kildare Limestone (Ashgill), Ireland, which was well described by Dean (1971). However, *O. kildarensis* is consistently different in having the glabellar furrows strongly incised across the median lobe, such that the frontal glabellar lobe is isolated from the posterior part of the glabella. In both *O. kildarensis* and *O. kingi* (see Kielan 1957) the axial furrows diverge forwards more strongly around the frontal lobe than they do in the Thai form, so that the outline of the furrows is curved in these species. The glabella presumably represents the plesiomorphic condition in which the furrows are more *Atractopyge*-like.

Family HAMMATOCNEMIDAE Kielan, 1960

Genus OVALOCEPHALUS Koroleva, 1959*a*

Type species. *Ovalocephalus kelleri* Koroleva, 1959*a*, Caradoc of Kazakhstan, by original designation.

Remarks. Zhou and Dean (1986, p. 776) noted that *Ovalocephalus* was likely to be the senior synonym of *Hammatocnemis* Kielan, 1960. Through the kindness of Dr Koroleva I have been

---

EXPLANATION OF PLATE 8

Figs 1–10. *Ovalocephalus plewesae* sp. nov. 1, 5–6, holotype, It 25518; cranidium, in dorsal, lateral and anterior views; × 10. 2, It 25522; incomplete cranidium, showing shallow S2; × 10. 3–4, It 25521; hypostome in ventral, × 12, and lateral, × 8, views, the latter showing wings. 8, It 25520; small cranidium; × 15. 7, 9, It 25524; pygidium, dorsal and lateral views; × 16. 10, It 25523; plan view of small, incomplete free cheek; × 10. All 18 m.

Fig. 11. *Josephulus gracilis* Warburg, 1925; cast of holotype, RM D-188, Swedish Museum of Natural History; cranidium; Boda Limestone (Ashgill), Sweden; × 5.

Fig. 12. *Parisoceraurus rectangularis* Zhou, 1977; It 25430; cranidium; 14·4 m; × 7.

Specimen details of figs 1–10, 12 as for Plate 1, figures 1, 3–12.

PLATE 8

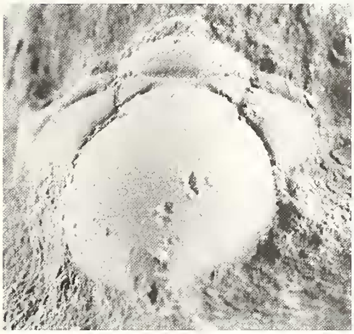

1


2


3

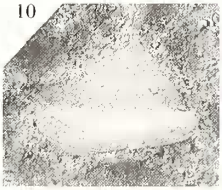

4


5


6


8


9


10


11


12

supplied with a photograph of the holotype of the type species, which is illustrated as Plate 9, figure 7 herein. These confirm the synonymy; the anterior glabellar furrows are more effaced on the type species of *Ovalocephalus* than on the type species of *Hammatocnemis*, *H. tetrasulcatus* Kielan, 1960, but this is a variable feature in the group and not of generic significance. Another genus which may belong in Hammatocnemidae is *Josephulus* Warburg, 1925; the type species, *J. gracilis*, is illustrated here (Pl. 8, fig. 11) from its cranidium, all that is described of it. It shares the distinctive glabellar shape of *Ovalocephalus tetrasulcatus*. It differs from all the species attributed to *Ovalocephalus* in having a narrow (sag.) occipital ring, long genal spines and a clearly distinct lateral border on the cranidium.

Ovalocephalus plewesae sp. nov.

Plate 8, figures 1–10

1988 *Ovalocephalus kelleri* Koroleva; Dean and Zhou, p. 776, pl. 64, figs 13–14 [sub *Hammatocnemis kelleri* [*sic*]].

Derivation of name. For Caryl Plewes, who helped the author with preparation of material.

Holotype. Cranidium, It 25518.

Paratypes. Cranidia, It 25520, 25522, 25476; hypostome, It 25521; free cheek, It 25523; pygidium, It 25524.

Stratigraphical range. Lower part of the Pa Kae Formation section, 0·6–18·0 m above base.

Diagnosis. *Ovalocephalus* having glabella produced into an anterior, spine-like 'nose'; S3 and S4 glabellar furrows effaced; surface sculpture lacking; genal spine present.

Description. The cranidium of this species lacks surface sculpture. All other *Ovalocephalus* species are granulose. Hence it is likely that the pygidium, free cheek and hypostome, are correctly assigned, because they are from the same horizon as the type cranidium, and also lack surface sculpture. Mature cranidium longer than wide. Much of this length is accounted for by the extension of the glabella into a long 'nose' anteriorly. On the small cranidium this extension is less pronounced, but a spine-like protuberance is clear. The glabella is less inflated than it is in other species of *Ovalocephalus*. Glabella tapers forwards to a point behind S2, then expands forwards to a maximum width which is about twice minimum width. Axial furrows are narrow. Glabellar furrows are also narrow, but distinct. Only two pairs are incised; S1 slopes inwards and backwards to approach the occipital furrow closely; S2 is shorter and is directed slightly anteriorly. Hence, the two furrows enclose an acute angle. There is a comparatively weak furrow running across the glabella connecting the inner ends of S1. A very faint third pair of glabellar furrows, isolated within the glabella, is shown by the larger specimen on Plate 8, figure 2. The occipital ring is very wide (sag.) and widest medially. The occipital furrow is narrow, and of equal depth along its length. The fixed cheeks are gently convex, more or less continuing the downward slope of the anterolateral part of the glabella. The posterior fixigenal border has about half the width (exsag.) of the occipital ring. Short, stout, pointed genal spine present. The free cheek (eye not preserved) has a smooth genal field, but a highly convex border carrying a few raised lines.

A hypostome (Pl. 8, figs 3–4) is similar to those (but perhaps better preserved) which have been associated with other species of *Ovalocephalus* (Lu and Zhou 1979, pl. 3, fig. 6; Dean and Zhou 1988, p. 57). Middle body gently convex with a pair of slightly depressed maculae weakly indicated at its mid-length, well isolated from the marginal furrows. Borders narrow and convex, widening gently backwards, and distinctly defined by narrow border furrows. Posterior margin carries a pair of posterolateral spines, and a median one is indicated.

The posterior thoracic segment is attached to the pygidium, showing gently convex axis narrower (tr.) than pleurae. Pleura divided into adaxial horizontal part, and lateral downsloping part with bluntly spinose termination. The adaxial part carries narrow (exsag.) posterior articulating ridge, which engages with boss on front of pygidium.

Pygidium more than twice as wide as long, broadly arched upward about mid-line. Axis tapers posteriorly, but its posterior end is not defined. The four axial rings are progressively shorter backwards (sag.) and the axial rings defining them also curve more markedly forwards medially. There are three pleural ribs: the first is completely defined, reaching the margin; the furrow defining the second does not curve backwards at its outer end, where it fades out before reaching the margin, the furrow defining the third is extremely short, present adaxially only.

Remarks. The type species, *O. kelleri* Koroleva, 1959*a* (see also Koroleva 1959*b*), has a less pointed frontal glabellar lobe than *O. plewesae*, and also a granulose surface sculpture, and its basal glabellar lobes are sub-circular and inflated. Chinese species attributed to this genus were reviewed by Lu and Zhou (1979), and none of these has the glabellar 'nose' of the new species, the S3 and S4 furrows are developed, and, where the cuticle is preserved, a granulose sculpture is general. The same distinctions apply to *O. hexianensis* (Q. Z. Zhang *in* Qiu *et al.* 1983) and *O. tetrasulcatus* (Kielan, 1960). Where genal spines are present at all on these species they are very short and stubby. The closest comparisons with *O. plewesae* are with species figured by Zhou and Dean (1986) from the Chedao Formation, Gansu. Their species, *H. obsoletus*, is likewise smooth, and the anterior glabellar furrows are similarly obsolete. However, its glabellar frontal lobe is rounded, and a genal spine is lacking from much wider (tr.) fixed cheeks, and it seems very unlikely that such consistent and prominent differences could be intraspecific. The pygidium attributed to *O. obsoletus* is much like that of *O. plewesae*. Zhou and Dean also recognized what they identified as *O. kelleri* Koroleva. The specimen on their plate 64, figures 13–14 is very like *O. plewesae*, and unlike *O. kelleri* both with regard to the outline of the glabellar frontal lobe and in having genal spines; the basal glabellar lobes are a little more inflated than in the Thai material and the furrow joining their inner ends is stronger, but the similarities are sufficient to indicate that they should be regarded as conspecific. The Gansu species is Caradoc in age.

Ovalocephalus ovatus (Sheng, 1964)

Plate 9, figures 1–6, 8, 12

1964	*Hammatocnemis tetrasulcatus* var. *ovatus* Sheng, p. 560, pl. 2, fig. 2*a–c*.
1975	*Hammatocnemis ovatus* Sheng; Lu, p. 441 (231), pl. 45, figs 1–3.
1975	*Hammatocnemis pagoda* Chen (*in* Li *et al.*), pl. 21, figs 7–8.
1977	*Hammatocnemis ovatus* Sheng; Wang and Jin (eds), p. 252, pl. 76, fig. 6.
1978	*Hammatocnemis ovatus* Sheng; Xia, p. 181, pl. 36, figs 6–7.
1986	*Hammatocnemis ovatus* Sheng; Xiang and Ji, p. 60, pl. 2, figs 13–14.
1986	*Hammatocnemis ovatus* Sheng; Ji, pl. 6, fig. 16.

Material. Cephalon, It 25290; cranidia, It 25178, 25223–25224, 25320–25321, 25398–25399, 25401, 25403, 25432–25434, 25474, 25526–25527, 25536–25544, 25519, 25891, 25893–25897; pygidia, It 25222, 25338, 25545, 25898–25899, 26203–26205; free cheeks, It 25221, 25291, 25380, 25405, 25546, 25548; hypostomes, It 25225, 25341, 25549, 26206; thoracic segments, It 25525, 25547, 25550.

Stratigraphical range. Throughout measured section of Pa Kae Formation.

Description. Thai material of this species is particularly well preserved, possibly the best for any species of the genus, and a description is therefore worthwhile. A description of the type material from the upper part of the Pagoda Formation was given by Sheng (1964), but his material was not well preserved. A fuller description by Lu (1975) cites the ovate anterior part of the glabella with convex-outward axial furrows as distinguishing *O. ovatus* from other species of the genus, features clearly seen on the Thai material. Lu's specimens are at least partly internal moulds, whereas the Thai material retains the exoskeleton. The glabellar furrows thus appear a little shorter and narrower. Four pairs are preserved, of which the first, transglabellar furrow is by far the deepest and the three anterior pairs are more or less evenly spaced along the axial furrows and very short. The anterior pair is shortest and is almost obsolete on some specimens. The deep axial furrows enclose an angle of 60–70°; they diverge in front of the circular basal glabellar lobes. The frontal lobe of the glabella considerably overhangs the very narrow anterior border. In dorsal view, the length of the glabella in front of S1 is equal to the maximum glabellar width in front of the palpebral lobes. The fragility of the limestone does not allow preparation of the ventral surface of the cephalon. The posterior border widens into a genal spine remnant. This is of interest because it shows that the suture can be considered homologically proparian (see also Hammann 1992, p. 106), even though the posterior branch of the facial suture cuts the posterior margin of the cephalon immediately outside the genal spine (Pl. 9, fig. 5). The genus was described as opisthoparian by Lu and Zhou (1979, p. 430) and Han (1980). As described above, the genal spine of *O. plewesae* is longer, and is also present on the cranidium. Lu and Zhou took the form of the facial suture as the defining character, because it reaches the posterior margin as in other opisthoparian trilobites. The species they described with cheeks in place lack noticeable genal spines. However, the recognition of the genal spines shows that in this unusual trilobite the posterior branch of the facial suture has shifted backwards. The alternative would be that the spines on *Ovalocephalus* were not homologous with 'normal' genal spines. While this is a possibility, it sits ill with the idea that *Ovalocephalus* is related to the proparian Cheiruridae, which Lu and Zhou (1979) argued from other grounds. The condition of the suture might be described as pseudo-opisthoparian.

The eye is convex, deep, and placed rather far forwards; in the cephalic orientation with the occipital ring horizontal it is inclined forwards. The eye lenses appear to be normal holochroal. The eye is elevated on a convex eye socle, which carries a few larger tubercles. The lateral border is steeply sloping and bevelled. Surface sculpture is generally finely granulose other than on borders, but with scattered larger tubercles on frontal lobe, on genae, and on the eye socle. The lateral border carries a few raised lines.

Four conjoined thoracic segments illustrate the high thoracic convexity and the cheirurid-like articulation and pleural spines. The pygidium is variable, up to three times as wide as long; terminal part of gently tapering axis effaced, anterior two rings clearly defined, a third may be well-developed, and a fourth faint on poorly preserved material. Similarly, the anterior three pairs of pleural spines are well differentiated but the third is often only indicated proximally.

Remarks. This species closely resembles the type species, *O. kelleri*, from the Caradoc of Kazakhstan (Koroleva 1959*a*, 1959*b*; Apollonov 1974, pl. 13, fig. 9; Pl. 9, fig. 7 herein). There are two points of distinction: the glabellar furrows anterior to the second pair are effaced in *O. kelleri*, and the divergence of the axial furrows in front of S1 is even lower; they enclose an angle of about 40°. This results in a longer frontal glabellar lobe, the length of the glabella in front of S1 exceeding its maximum transverse width. Hammann (1992, pl. 22, fig. 12) figured a cranidium from the Cystoid Limestone of Spain very like that of *O. ovatus* under the name *O.* cf. *tetrasulcatus*. *O. tetrasulcatus* (Kielan) (see for example, Kielan 1960, pl. 25, fig. 3; pl. 26, figs 2–4; pl. 27, figs 6–8; Apollonov 1974, pl. 13, figs 1–8; Lu and Zhou 1979, pl. 2, figs 10–11; Dean and Zhou 1988, pl. 59 figs 10, 12–16), the type species of *Hammatocnemis*, is also very similar, and is distinguished primarily by having angulate anterolateral corners of the glabella, which gives the anterior part of the glabella a sub-pentagonal outline in many specimens. I am uncertain if the apparently better definition of the glabellar furrows of *tetrasulcatus* might be attributable to differing preservation states. The better preserved of Kielan's specimens (1960, pl. 26, fig. 4) show a wider divergence of the axial furrows, up to 90°, but this is not the case with specimens such as that illustrated by Lu and Zhou (1979, pl. 2, fig. 10). There is apparently no genal spine remnant on *tetrasulcatus*. Also generally similar to *O. ovatus* is *O. decorosus* Lu (*in* Lu and Chang, 1974) (see Lu and Zhou 1979; Tripp *et al.* 1989), a species having a less forwardly bulbous glabella, and apparently only a third pair of well-defined pygidial pleural ribs. Some pygidia attributed to *tetrasulcatus* by Apollonov (1974, pl. 14, figs 1–6) also show clearly defined third ribs.

EXPLANATION OF PLATE 9

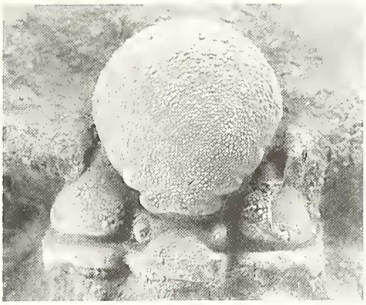
Figs 1–6, 8, 12. *Ovalocephalus ovatus* (Sheng, 1964). 1–2, 12, It 25474; well-preserved cranidium in dorsal, lateral and anterior views; 10·6 m; ×6. 3, It 25891; cranidium; 18 m; ×10. 4–5, It 25290; small cephalon, anterior and lateral views, the latter showing genal spine relative to facial suture; 18 m; ×8. 6, It 25338; pygidium; 39 m; ×5. 8, It 25291; free cheek, lateral view showing sculpture and eye; 18 m; ×12.

Fig. 7. *Ovalocephalus kelleri* Koroleva, 1959; holotype, Almaty Museum, Geological Institute, type collection; cranidium; Caradoc, Kazakhstan; ×3. Photograph kindly supplied by M. N. Koroleva.

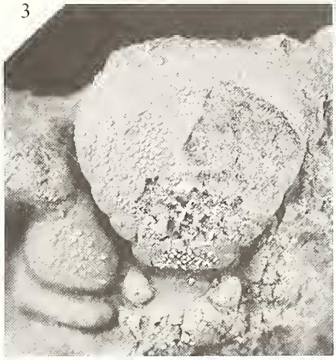
Figs 9–11. *Hadromeros xiushanensis* (Sheng, 1964). 9, It 25858; incomplete cranidium; 18 m; ×5. 10–11, It 25328; pygidium, dorsal and anterior views, showing angle of elevation of spines; 39 m; ×10.

Except for figure 7, details as for Plate 1, figures 1, 3–12.

PLATE 9

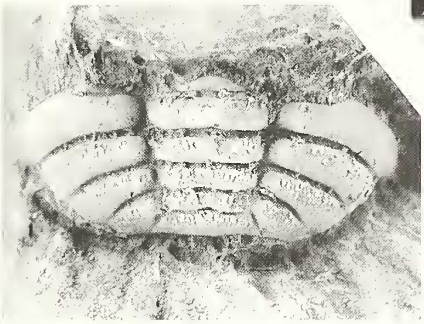

1


2

3



4


5


6

7

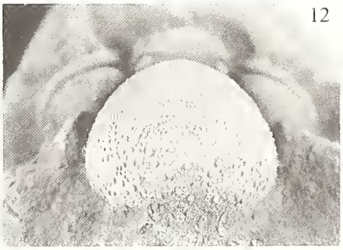


8


9


10


11

12


FORTEY, *Ovalocephalus*, *Hadromeros*

Family CHEIRURIDAE Hawle and Corda, 1847
Subfamily CHEIRURINAE Hawle and Corda, 1847

Genus HADROMEROS Lane, 1971

Type species. Cheirurus keisleyensis Reed, 1896, Ashgill, Cumbria, England, by original designation.

Remarks. The phylogenetics of the cheirurids are not well understood. Lane (1971, text-fig. 10) showed an evolutionary scheme which derived *Hadromeros* from *Xylabion*; the differences between these two genera as listed by Lane (1971, p. 24) are mostly plesiomorphic characters of the latter (parallel-sided glabella with relatively low convexity) which do not provide a satisfactory diagnosis. Late Ordovician cheirurines are often referred to *Hadromeros*, to which one species from Thailand is cautiously assigned. However, there is another genus, *Parisoceraurus* Zhou (*in* Wang and Jin, 1977) (see also Tripp *et al.* 1989), which is stated to differ from *Hadromeros* in having a cranidial border (like *Xylabion*), eyes somewhat farther forward, and exceptionally long 'great spines' on the pygidium (like *Ceraurus*). There is a narrow cranidial border on the species described below, and Zhou (*in* Wang and Jin 1977) described two species of *Parisoceraurus* which are not different from *Hadromeros xiushanensis* in this feature, and Zhou evidently wished to assign this species also to his new genus. Clearly, the whole group needs critical revision, but I cannot attempt this on the basis of the small amount of material available from Thailand.

Hadromeros xiushanensis (Sheng, 1964)

Plate 9, figures 9–11

1964 *Eccoptochile xiushanensis* Sheng, p. 548, pl. 3, fig. 1*a–c*.
1975 *Paraceraurus sinicus* Lu, p. 424, pl. 42, figs 9–10.
1975 *Paraceraurus longisulcatus* Lu, p. 425, pl. 42, fig. 11.
1986 *Hadromeros xiushanensis* (Sheng); Ji, p. 22, pl. 6, figs 8–9 (?*non* figs 6–7).

Materials. Cranidium, It 25858; pygidium, It 25328.

Stratigraphical range. Upper part of Pa Kae Formation section, 18–39 m above base.

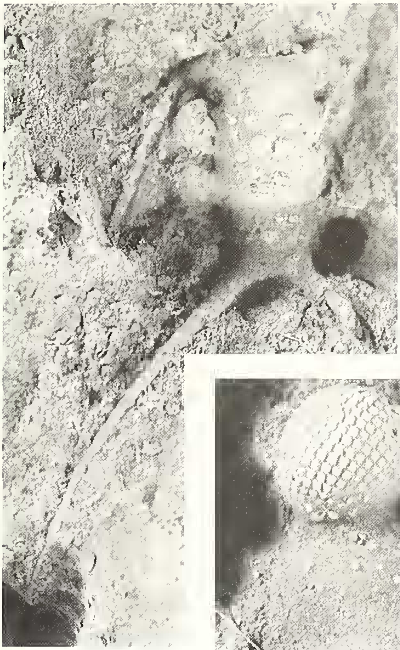
Remarks. Ji (1986) synonymized several species described from the Pagoda limestone in *H. xiushanensis*. An incomplete cranidium from Thailand shows straight, long, and very deep glabellar furrows considered typical of the species. I have also prepared a pygidium with elongate anterior spines and reduced median ones which P. D. Lane informs me (pers. comm. 1995) is typical of

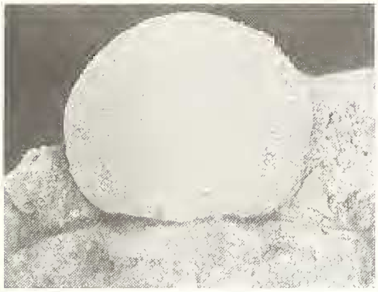
---

EXPLANATION OF PLATE 10

Fig. 1. *Miraspis* sp.; It 25888; cranidium; 18 m; × 10.
Figs 2–3, 5. *Sphaerexochus fibrisulcatus* Lu, 1975. 2–3, It 25494; cranidium, dorsal and anterior views; × 15. 5, It 25495; damaged cranidium; × 12. Both 42 m.
Figs 4, 6. *Hispaniaspis*? sp. indet. 4, It 25886; incomplete free cheek, lateral view; × 20. 6, It 25892; incomplete cranidium; × 20. Both 18 m.
Figs 8–9. *Oedicybele*. sp. nov. A; It 25477; cranidium, dorsal and anterior views; 0·6 m; × 8.
Figs 7, 10–11. *Oedicybele sulcata* (Lu, *in* Lu *et al.*, 1976); It 25887; cranidium, lateral, dorsal and anterior views: 42 m; × 12.
Fig. 12. *Lichas*? sp.; It 25443; hypostome incomplete on right side; 14·4 m; × 6.
Specimen details as for Plate 1, figures 1, 3–12.

PLATE 10


1


2


3


4


5


6

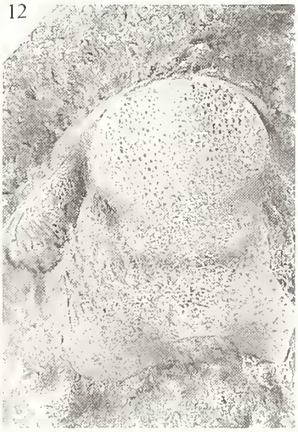

7


8


9


10


11


12

FORTEY, Ordovician trilobites

Hadromeros, and it seems natural to associate it with the cranidium. What is puzzling, however, is that this pygidium is quite different from that attributed to *H. xiushanensis* by Ji (1986, pl. 6, figs 6–7). This has three pairs of subequal spines, and rather subdued ring furrows. Given the depth of the glabellar furrows, an effaced axis does seem ill-suited for this species (and is unlike that of other *Hadromeros* species or Cheirurinae), and I think it likely that Ji's assignment is incorrect.

Genus PARISOCERAURUS Zhou, *in* Wang and Jin, 1977

Type species. Parisoceraurus rectangularis Zhou, 1977, Huangnehkan Formation, Ashgill, Jianxi, China, by original designation.

Parisoceraurus rectangularis Zhou, *in* Wang and Jin, 1977

Plate 8, figure 12

1977 *Parisoceraurus rectangularis* Zhou, *in* Wang and Jin, p. 251, pl. 75, figs 6–7.
?1978 *Eccoptochile*? sp. indet.; Kobayashi and Hamada, pl. 2, fig. 1.

Material. Cranidia, It 25430, 25471.

Stratigraphical range. Lower part of Pa Kae Formation section, 0·6–14·4 m above base.

Remarks. This species was described briefly from a cranidium. It is immediately distinguishable from that of *Hadromeros xiushanensis* in having short (tr.) glabellar furrows. Specimens from Thailand show similarly short furrows, and the palpebral lobe in anterior position opposite S3. The fixed cheeks are a little narrower than in the Chinese specimen. Forwardly placed palpebral lobes were considered a character that distinguished *Parisoceraurus* from *Hadromeros* (Tripp *et al*. 1989, p. 60), but as discussed above the generic placement of *xiushanensis* has varied. However, the cranidium discussed here is like that of *P. rectangularis* and does not resemble *xiushanensis*. *Parisoceraurus zhejiangensis* Ju (*in* Qiu *et al*., 1983) also has long (tr.) glabellar furrows. A fragmentary cranidium from Langkawi figured by Kobayashi and Hamada (1978, pl. 2, fig. 1) shows a similarly forward eye position and may belong to this species.

Subfamily SPHAEREXOCHINAE Öpik, 1937

Genus SPHAEREXOCHUS Beyrich, 1845

Sphaerexochus fibrisulcatus Lu, 1975

Plate 10, figures 2–3, 5

1975 *Sphaerexochus fibrisulcatus* Lu, pp. 218, 427, pl. 43, figs 1–4.
1977 *Sphaerexochus fibrisulcatus* Lu; Wang and Jin, p. 251, pl. 75, fig. 4.

Material. Cranidia, It 25213–25214, 25329–25331, 25473, 25494–25495.

Stratigraphical range. Pa Kae Formation, throughout measured section.

Remarks. This species was described originally by Lu (1975) from the upper part of the Pagoda Limestone from the Ichang district, Hubei. He thoroughly discussed differences from previous described species. Well-preserved cranidia from Thailand clearly show the diagnostic character: effacement of the lateral glabellar furrows. However, the occipital ring is well defined. S1 is visible as a faint, backward-curving line. This is unusual in sphaerexochines (indeed, all cheirurids), in which S1 is strongly incised, and I know of no other species with this feature. The surface sculpture comprises fine-scale tubercles.

Family LICHIDAE Hawle and Corda, 1847

Genus LICHAS Dalman, 1827

Types species. Lichas laciniatus (Wahlenberg), Dalmanites Shale (Ashgill), Sweden, by original designation.

Lichas? sp.

Plate 10, figure 12

Material. Hypostomes, It 25347, 25443.

Stratigraphical range. Pa Kae Formation section, 14·4–39·0 m above base.

Remarks. The only evidence for lichids is two well-preserved hypostomes, one of which is illustrated, this being the first proof of the family in the Ordovician of the Shan Thai block. It is of lichine form, and is tentatively assigned to *Lichas* on the basis of its similarity to the hypostome of *Lichas affinis* (Angelin) (e.g. Hammann 1992, pl. 29, fig. 5).

Family ODONTOPLEURIDAE Burmeister, 1843

Genus MIRASPIS Richter and Richter, 1917

Type species. Odontopleura mira Barrande, 1846, Liteň Formation (Wenlock), Bohemia, by original designation.

Miraspis sp. indet.

Plate 10, figure 1

Material. Cranidia, It 25888–25889.

Stratigraphical range. Pa Kae Formation, 18 m from the base of section.

Remarks. The odontopleurid material is incomplete, but is worth recording as the only example of the family from the Ordovician of the Shan Thai block. Ramsköld (1991) has revised many of the generic concepts in the family and listed species assignments. The figured small cranidium with long, paired occipital spines typical of *Miraspis* differs from the type species only in its wider median glabellar lobe, and very coarse surface sculpture (see, for example, Bruton 1966, pl. 7). Most other *Miraspis* species listed by Ramsköld are Silurian, but *M. solbergensis* Bruton, 1966, and *M. ceryx* Whittington and Bohlin, 1958 are Ashgill and Llanvirn respectively. The former has subdued sculpture and short occipital spines; the latter is much wider (tr.) than the Thai species. Both these species were erected on the basis of sparse material, but I am reluctant to add another by formally recognizing the Thai form from two cranidia.

Genus HISPANIASPIS Hammann, 1992

Types species. Hispaniaspis dereimsi Hammann, Ordovician (Ashgill), Cystoid Limestone, Spain, by original designation.

Hispaniaspis? sp. indet

Plate 10, figures 4, 6

Material. Cranidium, It 25892; possibly associated free cheek, It 25886.

Stratigraphical range. Pa Kae Formation section, 14·4–18·0 m above base.

Remarks. A well-preserved, small cranidium shows an inflated median glabellar lobe, subdued, but apparently fused lateral glabellar lobes, a large palpebral lobe placed in a posterior position, and apparently the circular base of a single, large median occipital spine. It seems unlikely that this spine forked distally in the manner of *Dicranurus* because such spines are produced by an extension of the entire occipital area, whereas the spine in the Thai specimen is discrete. A sculpture of scattered tubercles is associated with the median glabellar lobe and the fixed cheeks. I have very tentatively associated a free cheek from the same bed showing a similar sculpture beneath the eye, which is also appropriately large. L. Ramsköld (pers. comm. 1995) has indicated to me that the combination of cranidial characters is unusual and that the Thai form may represent a new genus. The material at hand is not adequate to name it. The inflated median glabellar lobe can be compared to that of *Whittingtonia* (e.g. Hammann 1992, pl, 31, fig. 3), but the fusion and effacement of the lateral lobes is different, as is the single occipital spine and large size of the palpebral lobes and posterior position of the eye. *Hispaniaspis* is known only from the Spanish type species, and it, too, has paired occipital spines, although the median 'tubercle', with which the occipital spine is presumably homologous, is also prominent. *H. dereimsi* does have the eye in a similar position to the Thai species, but its lateral glabellar furrows are not fused. A free cheek (Hammann 1992, pl. 32, fig. 4) is generally like the one from Thailand, having a wide and flat exterior border, although the eye is evidently considerably smaller. I have opted to refer the Thai species with question to *Hispaniaspis*, under open nomenclature. This interesting species would clearly repay further research.

Acknowledgements. I am indebted to Thanis Wongwanich and Clive Burrett for inviting me to study this fauna, and for guiding me in the field. Dr S. Bunopas approved field support from the Geological Survey of Thailand, without which the work would have been impossible. On a subsequent occasion (1994) Art Boucot supported my visit to the locality, and I express my debt both to him and to the National Science Foundation. For taxonomic advice I thank Phil Lane, Bob Owens, Lars Ramsköld and Zhou Zhi-qiang. Caryl Plewes ably assisted with the preparation of specimens, and Claire Mellish with the diagrams.

REFERENCES

AHLBERG, P. 1989. Agnostid trilobites from the Upper Ordovician of Sweden and Bornholm, Denmark. *Bulletin of the Geological Society of Denmark*, **37**, 213–226.

ANGELIN, N. P. 1854. *Palaeontologia Scandinavica, Part 1. Crustacea Formationis Transitionis*, Appendix. Lipsiae, Lund, 21–92, pls 25–41.

APOLLONOV, M. K. 1974. [*Ashgill trilobites of Kazakhstan*.] Nauka Kazakhskoij SSR, Alma Ata, 136 pp., 21 pls. [In Russian].

BALDIS, B. and POTHE DE BALDIS, E. D. 1995. Trilobites Ordovicicos de la Formacion Las Aguafditas (San Juan, Argentina) y consideraciones estratigraficas. *Boletin de la Academia Nacional de Ciencias, Cordoba*, **60**, 409–435, pls 1–7.

BANCROFT, B. B. 1949. Upper Ordovician trilobites of zonal value in southeast Shropshire. *Proceedings of the Royal Society of London, Series B*, **136**, 291–315, pls 9–11.

BARRANDE, J. 1846. *Notice préliminaire sur le système silurien et les trilobites de Bohême*. Bellman, Leipzig. vi+91 pp.

—— 1852. *Système silurien de la Bohême. 1ère partie. Recherches Paléontologiques*. C. W. Medau, Prague and M. M. Gottlieb Haase fils, Paris, 935 pp., 541 pls.

BEYRICH, E. 1845. *Über einiger böhmischen Trilobiten*. Berlin, 47 pp., 1 pl.

BILLINGS, E. 1865. Palaeozoic fossils, vol. 1. *Geological Survey of Canada*. Ottawa, 426 pp.

BRUTON, D. L. 1966. A revision of the Swedish Ordovician Odontopleuridae (Trilobita). *Bulletin of the Geological Institutions, University of Uppsala*, **43** (8), 1–40, pls 1–6.

—— 1968. The trilobite genus *Panderia* from the Ordovician of Scandinavia and the Baltic areas. *Norsk Geologisk Tidsskrift*, **48**, 1–34, pls 1–12.

—— 1976. The trilobite *Phillipsinella* in the Ordovician of Great Britain and Scandinavia. *Palaeontology*, **19**, 699–714, pls 104–108.

—— and OWEN, A. W. 1988. The Norwegian Upper Ordovician illaenid trilobites. *Norsk Geologisk Tidsskrift*, **68**, 241–258.

BURMEISTER, H. 1843. *Die organisation der Trilobiten aus ihren lebenden Verwandten entwickelt; nebst einer systematischen Uebsersicht aller zeither beschriebenen Arten.* Berlin, xx + 147 pp., 6 pls.

BURRETT, C. F., LONG, J. and STAIT, B. 1990. Early–Middle Palaeozoic biogeography of Asian terranes derived from Gondwana. 163–174, *In* McKERROW, W. S. and SCOTESE, C. R. (eds). *Palaeozoic palaeogeography and biogeography.* Memoirs of the Geological Society of London, 13, 435 pp.

BURST, J. F. 1965. Subaqueously formed shrinkage cracks in clay. *Journal of Sedimentary Petrology*, **35**, 348–353.

CHEN XU, RONG JIA-YU, WANG XIAO-FENG, WANG ZHI-HAO, ZHANG YUAN-DONG and ZHAN REN-BIN 1995. Correlation of the Ordovician rocks of China. *International Union of Geological Sciences Publication*, **31**, 1–104.

COCKS, L. R. M. and FORTEY, R. A. 1988. Lower Palaeozoic facies and faunas around Gondwana, 183–200. *In* HALLAM, A. and AUDLEY-CHARLES, M. (eds). *Gondwana and Tethys.* Special Publications of the Geological Society, London, 37, 317 pp.

—— and RONG JIA-YU 1988. A review of the later Ordovician *Foliomena* brachiopod fauna. *Palaeontology*, **31**, 53–67.

DALMAN, J. W. 1827. Om palaeaderna eller de så kallade Trilobiterna. *Kunglinga Svenska Vetenskapsakademiens Handlingar*, 113–152, 226–294, pls 1–6. [For 1826].

DEAN, W. T. 1963. The Ordovician faunas of South Shropshire, 3. *Bulletin of the British Museum* (*Natural History*), *Geology Series*, **7**, 213–254, pls 37–46.

—— 1967. The distribution of Ordovician shelly faunas in the Tethyan region. 11–44. *In* ADAMS, C. G. and AGER, D. V. (eds). *Aspects of Tethyan biogeography.* Systematics Association Publication, 7, London, 336 pp.

—— 1971 Trilobites of the Chair of Kildare Limestone (Upper Ordovician) of eastern Ireland. Part 1. *Monograph of the Palaeontographical Society*, **125** (531), 1–64, pls 1–25.

—— and ZHOU ZHI-YI 1988. Upper Ordovician trilobites from the Zap Valley, south-east Turkey. *Palaeontology*, **31**, 621–649.

DOLAMBI, T. and GOND, P. 1991. *Aocaspis* nov. gen., nouveau trilobite Nileidae de l'Ordovicien Inferieur de Montagne Noire (France). *Géobios*, **25**, 213–224.

FORTEY, R. A. 1975*a*. Early Ordovician trilobite communities. *Fossils and Strata*, **4**, 331–352.

—— 1975*b*. The Ordovician trilobites of Spitsbergen. 2. Asaphidae, Nileidae, Raphiophoridae and Telephinidae of the Valhallfonna Formation. *Skrifter Norsk Polarinstitutt*, **162**, 1–125, pls 1–41.

—— 1980. The Ordovician trilobites of Spitsbergen. 3. Remaining trilobites of the Valhallfonna Formation. *Skrifter Norsk Polarinstitutt*, **171**, 1–113, pls 1–25.

—— 1985. Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **76**, 219–231.

—— 1990. Ontogeny, hypostome attachment and trilobite classification. *Palaeontology*, **33**, 529–576.

—— and CLARKSON, E. N. K. 1976. The function of the glabellar 'tubercle' in *Nileus* and other trilobites. *Lethaia*, **9**, 101–106.

—— HARPER, D. A. T., INGHAM, J. K., OWEN, A. W. and RUSHTON, A. W. A. 1995. A revision of Ordovician series and stages from the historical type area. *Geological Magazine*, **132**, 15–30.

—— and OWENS, R. M. 1987. The Arenig Series in South Wales. *Bulletin of the British Museum* (*Natural History*), *Geology Series*, **41**, 69–307.

—— and WILMOT, N. 1991. Trilobite cuticle thickness in relation to palaeoenvironment. *Paläontologische Zeitschrift*, **65**, 141–151.

FU LI-PU HU, YUN-XU, ZHANG ZI-FU and WANG SHU-XI 1993. The mark on the ecology of the sedimentary environment in Middle and Upper Ordovician at Ordos Basin. *Northwest Geoscience*, **14**, 1–88, pls 1–8 [In Chinese, English summary].

HAMMANN, W. 1992. The Ordovician trilobites from the Iberian Chains in the province of Aragon, NE-Spain. 1. The trilobites of the Cystoid Limestone (Ashgill Series). *Beringeria*, **6**, 1–144, pls 1–37.

HAN NAI-REN 1980. [On the carapace of *Hammatocnemis* Kielan.] *Geological Review, Beijing*, **26**, 183–189, pls 1–2 [In Chinese].

HAWLE, I. and CORDA, A. J. C. 1847. *Prodrom einer monographie der böhmischen trilobiten.* Prague, 176 pp., 7 pls.

HENRY, J.-L. 1994. The trilobites of the 'affaire Deprat'. *Alcheringa*, **18**, 359–362.

HORNÝ, R. and BASTL, F. 1970. *Type specimens of fossils in the National Museum, Prague, Volume 1, Trilobita.* National Museum, Prague. 354 pp., 20 pls.,

HOWELL, B. F. 1935. Cambrian and Ordovician trilobites from Herault, southern France. *Journal of Paleontology*, **9**, 222–238, pl. 23.

HU CHUNG-HUNG 1971. Ontogeny and sexual dimorphism of Lower Paleozoic Trilobita. *Palaeontographica Americana*, **44**, 1–130, pls 1–26.

HUNT, A. S. 1967. Growth, variation and instar development of an agnostid trilobite. *Journal of Paleontology*, **41**, 203–208.

JAEKEL, O. Über die Agnostiden. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **61**, 380–401.

JI ZAI-LIANG 1982. [Stratigraphical distribution and range of the trilobite Family Phillipsinellidae in South China.] *Bulletin of the Institute of Geology, Chinese Academy of Geological Sciences*, **6**, 57–68, pls 1–2. [In Chinese].

—— 1985. [On the depositional environment of the Pagoda Formation in central and southwestern China.] *Professional Papers in Palaeontology and Stratigraphy*, **12**, 87–93, pls 1–2. [In Chinese].

—— 1986. [Upper Ordovician (middle Caradoc–early Ashgill) trilobites from the Pagoda Formation in South China.] *Professional Papers in Palaeontology and Stratigraphy*, **15**, 1–33, pls 1–6. [In Chinese].

KIELAN, Z. 1957. On the trilobite family Staurocephalidae. *Acta Palaeontologica Polonica*, **2**, 155–180, pls 1–6.

—— 1960. Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. *Palaeontologia Polonica*, **11**, 1–198, pls 1–36.

KOBAYASHI, T. 1939. On the agnostids. *Journal of the Faculty of Science, Tokyo University, Section 2*, **5**, 66–198.

—— and HAMADA, T. 1970. Contributions to the geology and palaeontology of SE Asia. 78. A cyclopygid-bearing Ordovician faunule discovered in Malaysia with a note on the Cyclopygidae. *Geology and Palaeontology of Southeast Asia*, **8**, 1–18, pls 1–2.

—— —— 1978. Upper Ordovician trilobites from the Langkawi Islands, Malaysia. *Geology and Palaeontology of Southeast Asia*, **19**, 1–28, pls 1–2.

KOROLEVA, M. N. 1959*a*. [New genera of trilobites from the Middle and Upper Ordovician of northern Kazakhstan.] *Doklady Akademia Nauk SSSR*, **124**, 1313–1316. [In Russian].

—— 1959*b*. [New trilobites from the upper Ordovician (Caradoc) of Northern Kazakhstan.] *Sbornik Kazakhskogo gorno-metallurgicheskogo Instituta*, **20**, 75–113, pls 1–4. [In Russian].

—— 1982. [*Ordovician trilobites of north-east Kazakhstan.*] Ministry of geology of the Kazakh SSR (KazIMS). Moscow, 152 pp, 26 pls. [In Russian].

LAND, M. F. 1981. Optical mechanisms in the higher Crustacea with a comment on their evolutionary origins, 31–48. *In* LAVERACK, M. S. and COSENS, D. S. (eds). *Sense organs*. Blackie, Glasgow, 289 pp.

—— 1984. Crustacea. 401–438. *In* ALI, M. A. (ed.). *Photoreception and vision in invertebrates*. Plenum, New York, 853 pp.

LANE, P.D. 1971. British Cheiruridae (Trilobita). *Monograph of the Palaeontographical Society*, **125** (530), 1–95, pls 1–16.

LEONE, F., HAMMANN, W., LASKE, R. SERPAGLI, E. and VILLAS, E. 1991. Lithostratigraphical units and biostratigraphy of the post-Sardic Ordovician sequence in southwestern Sardinia. *Bolletina della Sociéta Paleontologica Italiana*, **30**, 201–235.

LI YAO-XI, SONG LI-SHENG, ZHOU ZHI-QIANG and YANG JING-YAO 1975. [*Early Palaeozoic stratigraphy of the western section of Tapa Mountain.*] Earth Sciences Publishing House, Beijing, 232 pp., 70 pls. [In Chinese].

LINNARSSON, J. G. O. 1869. Om Västergötlands Cambriska och Siluriska aflagringar. *Kongliga Svenska Vetenskaps-Akadiemens Handlingar*, **8**, 1–89, pls 1–2.

LU YAN-HAO 1957. Trilobita, 249–294, pls 137–155. *In* [*Index fossils of China, Invertebrate.*] Institute of Palaeontology Academica Sinica. [In Chinese].

—— 1962. [*Index fossils of the Yangtze Region.*] Science Press, Beijing. [In Chinese].

—— 1964. [*Handbook of Index fossils of Southeast China*] Science Press, Beijing. [In Chinese].

—— 1975. Ordovician trilobite faunas of central and southwestern China. *Palaeontologica Sinica, New Series B*, **11**, 1–463, pls 1–50.

—— and CHANG WEN-TANG 1974. [Ordovician trilobites.] *In* [*A handbook of stratigraphy and palaeontology in southwest China.*] Science Press, Beijing. [In Chinese].

—— CHU CHAO-LING, CHIEN YI-YUAN, ZHOU ZHI-YI, CHEN JUN-YUAN, LIU GENG-WU, YU WEN, CHEN XU and XU HAN-KUI 1976, Ordovician biostratigraphy and palaeozoogeography of China. *Memoirs of the Nanjing Institute of Geology and Palaeontology*, **7**, 1–83, pls 1–14. [In Chinese, English summary].

—— and ZHOU ZHI-YI 1979. [Systematic position and phylogeny of *Hammatocnemis* (Trilobita).] *Acta Palaeontologica Sinica*, **18**, 415–433, pls 1–4. [In Chinese].

—— —— 1981. [Early Upper Ordovician trilobites from the Nanjing Hills]. *Bulletin of the Nanjing Institute of Geology and Palaeontology*, **3**, 1–27, pls 1–7. [In Chinese].

MAREK, L. 1952. Contribution to the stratigraphy and faunas of the upper part of the Kralův Dvůr Shales (Ashgillian). *Sbornik Ustredniho Ustavu Geologického*, **19**, 429–455.

—— 1960. The trilobite family Cyclopygidae Raymond in the Ordovician of Bohemia. *Rozpravy Ustredního Ústavu Geologického*, **28**, 1–85, pls 1–6.

M'COY, F. 1845. *A synopsis of the Silurian fossils of Ireland.* Sir R. J. Griffith, Dublin, 72 pp., 5 pls.

METCALFE, I. 1992. Ordovician to Permian evolution of Southeast Asian terranes: NW Australian Gondwana connections, 293–306. *In* WEBBY, B. D. E. and LAURIE, J. R. (eds). *Global perspectives on Ordovician geology.* A. A. Balkema, Rotterdam, 513 pp.

MILLER, S. A. 1889. *North American geology and palaeontology.* Mattocks, Cincinnati, 664 pp.

MOORE, R. C. (ed.). 1959. *Treatise on invertebrate paleontology. Part O. Arthropoda 1.* University of Kansas Press and Geological Society of America, Lawrence, Kansas, 560 pp.

MORRIS, S. F. 1988. A review of British trilobites, including a synoptic revision of Salter's monograph. *Monograph of the Palaeontographical Society*, **140** (574), 1–316.

NIELSEN, A. T. 1995. Trilobite systematics, biostratigraphy and palaeoecology of the Lower Ordovician Komstad Limestone and Huk Formations, southern Scandinavia. *Fossils and Strata*, **38**, 1–374.

NIKOLAISEN, F. 1983. The Middle Ordovician of the Oslo Region, Norway, 32. Trilobites of the family Remopleurididae. *Norsk Geologisk Tidsskrift*, **62**, 231–299, pls 1–15.

ÖPIK, A. A. 1937. Trilobiten aus Estland. *Acta et Commentationes Universitatis Tartuensis*, **32**, 1–137, pls 1–26.

OWEN, A. W. and BRUTON, D. L. 1980. Late Caradoc–early Ashgill trilobites of the central Oslo Region, Norway. *Palaeontological Contributions of the University of Oslo*, **245**, 1–42, pls 1–10.

—— BRUTON, D. L., BOCKELIE, J. F. and BOCKELIE, T. G. 1990. The Ordovician successions of the Oslo Region, Norway. *Special Publication of the Norwegian Geological Survey*, **4**, 1–54.

OWENS, R. M. 1973*a*. Ordovician Proetidae (Trilobita) from Scandinavia. *Norsk Geologisk Tidsskrift*, **53**, 117–181.

—— 1973*b*. British Ordovician and Silurian Proetidae (Trilobita). *Monograph of the Palaeontographical Society*, **127** (535), 1–98, pls 1–15.

—— 1979. The trilobite genera *Panarchaeogonus* Opik, *Isbergia* Warburg and *Cyamops* gen. nov. from the Ordovician of Balto-Scandia and the British Isles. *Norsk Geologisk Tidsskrift*, **58**, 199–219.

—— and HAMMANN, W. 1990. Proetide trilobites from the Cystoid Limestone (Ashgill) of NW Spain, and the suprageneric classification of related forms. *Paläontologische Zeitschrift*, **64**, 221–244.

PEK, I. 1977. Agnostid trilobites of the central Bohemian Ordovician. *Sborník Geologických Věd*, **1977** (1), 7–44, pls 1–12.

—— and PROKOP, R. J. 1984. New finds of the agnostid trilobites from the Ordovician of the Prague area (Czechoslovakia). *Časopis Narodního Muzea*, **153**, 17–20, pl. 1.

PORTLOCK, J. F. 1843. *Report on the geology of the Country of Londonderry, and of parts of Tyrone and Fermanagh.* Geological Survey of Ireland, Dublin and London, xxi+784 pp., 54 pls.

PRANTL, F. and PŘIBYL, A. 1948. Classification of some Bohemian Cheiruridae. *Sborník Narodního Muzea v Praze*, **3B**, 1–44.

PRICE, D. and MAGOR, P. M. 1984. The ecological significance of variation in the generic composition of Rawtheyan (late Ordovician) trilobite faunas from North Wales, UK. *Geological Journal*, **19**, 187–200.

QIU, HONG-AN and 10 others. 1983. [*Paleontological Atlas of eastern China. 1. Lower Palaeozoic.*] Geological Press, Beijing, 657 pp., 176 pls. [In Chinese].

RAMSKÖLD, L. 1991. Pattern and process in the evolution of the Odontopleuridae (Trilobita). The Selenopeltinae and Ceratocephalinae. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **82**, 143–181.

RAYMOND, P. E. 1925. Some trilobites of the lower Middle Ordovician of eastern North America. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **47**, 1–180.

REED, F. R. C. 1896. The fauna of the Keisley Limestone. Part 1. *Quarterly Journal of the Geological Society, London*, **52**, 401–437.

—— 1935. The Lower Palaeozoic trilobites of Girvan. Supplement No. 3. *Monograph of the Palaeontographical Society*, **88** (400), 1–64, pls 1–4.

RICHTER, R. and RICHTER, E. 1917. Uber die Einteilung der Familie Acidaspidae und über einige ihrer devonischen Vertreter. *Zentralblatt für Mineralogie, Geologie und Paläontologie*, **1917**, 462–472.

SALTER, J. W. 1864. A monograph of the British trilobites from the Cambrian, Silurian and Devonian formations. Part 1. *Monograph of the Palaeontographical Society*, **16** (67), 1–80, pls 1–6.

SARS, G. O. 1835. Uber einige neue oder unvollständig bekannte trilobiten. *Isis*, **4**, 333–43, pl. 9.

SCHRANK, E. 1972. *Nileus*-Arten (Trilobita) aus Geschieben des Tremadoc bis tieferen Caradoc. *Berichte der Deutschen Gesellschaft für Geologische Wissenschaften, Berlin*, **17**, 351–375.

SHENG SHEN-FU. 1964. Upper Ordovician trilobite faunas of Szechuan-Kweichow with special discussion on the classification and boundaries of the Upper Ordovician. *Acta Palaeontologica Sinica*, **12**, 553–581.